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Facing social threats in adolescents with autism spectrum disorders

Christina Ioannou

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THÈSE DE DOCTORAT

de l'Université de recherche Paris Sciences et Lettres
PSL Research University

Ecole Normale Supérieure

Facing social threats in adolescents with autism spectrum disorders.
Percevoir et agir face à la menace sociale: études chez des adolescents atteints de troubles du spectre de l'autisme.

Ecole doctorale n°158

Cerveau Cognition Comportement

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“Everyone knows what an emotion is, until asked to give a definition.”

Fehr and Russell, 1984

1



“The most interesting people you’ll find are ones that don’t fit into your average cardboard box. They’ll make what they need, they’ll make their own boxes”

Dr. Temple Grandin.

¹ Original image “Autism” by [Hepingting](#) used under [CC BY-SA](#). Accessed June 2nd 2017.

Abbreviations

Autism Spectrum Disorders (ASD).....	10
Childhood Disintegrative Disorder (CDD).....	16
Diagnostic and Statistical Manual of Mental Disorders V (DSM-5).....	10
Event-Related Potential (ERP).....	40
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Foreword

The overall aim of this thesis is to investigate the perception of social threats in adolescents with and without autism and the behavioural regulation of each group in response to those threats. More precisely this thesis attempts to answer the question: can adolescents with autism process socio-emotional cues which signal threat? And if yes, can they adapt their behaviour in response to those signals in a way that it is advantageous for survival and/or social integration?

Autism is characterised by atypical perception of facial affect but the findings remain inconsistent in regard to the roots of such difficulties. While the literature is dominated by suggestions of a core emotion processing deficit in autism, a review from a methodological perspective reveals that under specific conditions, when individuals with ASD are not disadvantaged in comparison to controls, their emotion processing abilities appear preserved. Two relatively new hypotheses attempt to provide answers: 1) the behavioural self-regulation account (Bachevalier & Loveland, 2006; Hellendoorn, 2014; Loveland, 2005; Loveland, 2001) proposes that not only the mechanism behind the processing of emotional signals could be deficient in autism, but the mechanism behind the preparation of appropriate responses to those signals could be impaired too. And 2) the social motivation account (Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012; Dawson, Webb, & McPartland, 2005) which proposes that individuals with autism are characterised by deficits in the motivation/reward related system, which manifest through diminished social orienting, wanting and maintaining, and lead to the observed emotion perception deficits. According to this account, the actual mechanisms behind the processing of and/or responding to emotional signals remain intact but their engagement is not spontaneous. Given the above, studies with specific methodological constraints which serve as motivating conditions for the ASD group, should be able to disentangle at least partly between the two hypotheses and shed light into the emotion perception abilities of this group. If hypothesis one is the case then we would expect adolescents with autism to fail at one or both stages of the perception-action link, while if the second hypothesis were true, under well-controlled conditions, adolescents with autism should be able to process and respond to social threats similarly to controls.

Although, we could assess the perception of and responses to a wide range of emotions rather than specifically threatening ones, we focused on fear and anger because their facial expressions have evolved to signal threat, to communicate a direct message to the observer regarding the state of the emitter and to directly influence the observer's behaviour (Darwin, 1872; Dezechache, Mercier, & Scott-Phillips, 2013; Fridlund, 1994; Keltner & Haidt, 1999). Importantly, those emotions although they both signal threat and would be expected to induce avoidance tendencies in the observer, they differ in the action tendencies that they signal. Anger favours avoidance behaviours because it enhances strength

cues (Sell, Cosmides, & Tooby, 2014) and signals aggression (Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007) while fear favours approach behaviours because when it is directed to the observer it signals vulnerability (Hammer, & Marsh, 2015). Thus, they offer an ideal case for assessing the processing and responding to other's emotional signals and for investigating potential alternatives, such as emotion specific or action-tendencies specific deficits. Lastly, although we could assess those abilities in children, adolescents and/or adults we chose adolescent groups because this is a period developmentally distinct from the others when reactivity to threats is increased in comparison to children and adults in typical development (Hare et al., 2008).

To sum up, this doctoral work is dedicated to the investigation of the perception of social threats in adolescents with autism and specifically in providing answers to two pressing questions: 1) Can adolescents with autism process social threats? And if yes, 2) can adolescents with autism use social threats to adapt their behaviour accordingly?

Chapter 1: General Introduction

This chapter aims to provide a definition of autism and offer a review of the literature on face perception and emotion decoding in individuals with autism as compared to neurotypical controls. Firstly, I will give a brief historical overview of the definition of autism over the years. Secondly, I will attempt to explain why face perception is important for efficient social interaction and why it is important to study face perception in autism. Thirdly, I will summarise the literature regarding the perception of facial expressions of emotions in individuals with autism as compared to neurotypical individuals and the theories behind the atypical perception of facial affect characteristic of this group. The aim of this chapter is to ascertain the gaps in the literature on facial affect perception in autism and define the objectives of the present Ph.D. work.

1.1 Autism spectrum disorders

The word *autism* derives from the ancient Greek word *αὐτός* (*autos*) which means *self* and when connected with the suffix *-ism* it is used to describe “*a tendency towards the self*”. The first use of the word autism was as early as 1910 by Paul Eugen Bleuler who used it to describe one of the symptoms of schizophrenia; precisely the tendency to withdraw from the outside world into one of privacy (Fusar-Poli & Politi, 2008; Kuhn, 2004). In 1911, Bleuler introduced the term *autistic thinking*, a mode of free association thinking which was in contrast with what was considered the logical or realistic thinking mode. Consequently, the early definitions of autism were pointing to a type of infantile schizophrenia, an idea that was abandoned later on, when autism joined the group of neurodevelopmental conditions. It was not until 1943 that the term autism and the autistic thinking were linked to a set of behaviours, characteristic of disturbances of affective contact (Kanner, 1943). Soon after, in 1944, Asperger would use autism to refer to children who were egocentric and socially isolated (Frith, 1991) and would introduce the term “Asperger’s syndrome” to refer to a subgroup of individuals with autism, who were high functioning and “gifted”; they had distinctive abilities in one particular domain each which was later identified as savant syndrome, and is independent but highly comorbid with autism. Given the existence of several subgroups with different levels of symptom severity – all of which presented the characteristic socio-emotional difficulties alongside other symptoms, such as repetitiousness, rigidity, stereotypy, echolalia - autism changed from being referred to as a single construct to a spectrum of symptomatology, what we now refer to as autism spectrum disorders (ASD)

Since the publication of the fifth edition of the diagnostic and statistical manual of mental disorders (DSM-5; American Psychiatric Association, 2013) the term ASD refers to a cluster of lifelong neurodevelopmental conditions, which affect approximately 1% of the population (Elsabbagh et al.,

2012; Matson & Kozlowski, 2011; Saemundsen, Magnússon, Georgsdóttir, Egilsson, & Rafnsson, 2013), and are characterised by repetitive and restricted interests, pervasive impairments in reciprocal social interaction and difficulties in communication. They appear early in the life span of the individual and can be diagnosed from the second year of life, but manifest fully with age, as social demands increase and exceed the persons' capacities (American Psychiatric Association, 2013). The first full characterisation of ASD included the above triad of impairments, namely deficits in social interaction, impaired communication and repetitive/restricted interests which were considered interlinked and thought to co-occur (Wing & Gould, 1979). However, subsequent research found a very weak association between the social and non-social components affected in ASD (Happé, Ronald, & Plomin, 2006; Ronald, Happé, & Plomin, 2005; Ronald, Happé, Price, Baron-Cohen, & Plomin, 2006), suggesting the existence of distinct causes for the two impaired domains in this group and leading to the merging of the ASD characteristics into two components; one being the repetitive and stereotyped interests, or the non-social component and the second one the socio-communicative difficulties – the social component (American Psychiatric Association, 2013). Regardless of the number of different subgroups of people with autism that have been identified over the years, or the changes in evaluations and diagnostic criteria, what becomes clear is that a social deficit is at the core of the condition.

One of the most prominent characteristics of the social difficulties in this group is a general inattention to and an overall lack of interest in the social world or more specifically in social stimuli, the most salient of them being the human face (Dawson, Webb, & McPartland, 2005; Jemel, Mottron, & Dawson, 2006; Nomi & Uddin, 2015; Osterling, Dawson, & Munson, 2002; Osterling & Dawson, 1994, Chevallier, Huguet, Happé, George, & Conty, 2013; Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012). This had been reported as early as 1943 by Kanner (1943) who noted that these children, characterised by autistic behaviour, exhibited atypical eye-contact and a general indifference to the face of the other. In typical development, a social interest plays a vital role in the development of social abilities such as accurate face perception (Gliga & Csibra, 2007; Grelotti, Gauthier, & Schultz, 2002). Thus, absence of a social interest is considered socially detrimental. Given the existence of face specialisation brain areas, such as the fusiform gyrus, the amygdala or the superior temporal sulcus, it would be reasonable to suggest that humans show a biological predisposition for face expertise, but only provided that there is motivation to do so; provided there is a social interest at a personal level to look and interact with others, which in typical development encompasses infants' and young children's desire to look at faces (Grelotti et al., 2002; Haxby, Hoffman, & Gobbini, 2000). Given that an indifference towards faces appears from the first year of life in ASD (Osterling et al., 2002), it has been proposed that individuals with ASD might lack the proficiency and expertise of neurotypicals in face perception, which could be directly linked to their deficits in the perception of facial affect.

1.2 Why the face and why in autism? The case of facial expressions of emotion.

But why is face perception so important for effective social interaction and communication that if impaired it could be considered pivotal for the symptomatology of ASD? Accurate perception of human faces is considered the cornerstone for successful interpersonal communication (Schultz et al., 2000). Generally, human faces are the first thing that people encode when they meet others and the first thing that comes to mind when thinking of others. Humans have a vast memory capacity for encoding and maintaining not only a large number of faces but also their changeable characteristics and their meaning. Typically developing (TD) infants have a spontaneous preference for attending to the faces of others from the first year of life (Morton & Johnson, 1991) and neurotypical individuals are known to be experts in evaluating faces based on their traits. Faces are sources of information allowing us to determine another's identity but this alone could not explain the particular attraction of humans to the face of the other. Taking into account that faces are primarily perceived during online social interactions, the reason that they attract so much attention appears to be the wealth of social information that they offer to the observer regarding the emitter's state, mood and intentions (Haxby et al., 2000). This renders faces highly salient social stimuli.

Importantly emotions are principally, though not exclusively, expressed in the face. Facial expressions of emotion are known to serve functions essential for establishing social interaction, social learning and adaptation (Csibra & Gergely, 2011; Gergely, Egyed, & Király, 2007; Hess & Bourgeois, 2010). Emotions are multifaceted phenomena, the definition of which has always dependent upon whom you ask and at which point in time. From an evolutionary perspective, which is adopted in the present doctoral work, emotions are (Nesse 1990): *“specialized modes of operation shaped by natural selection to adjust physiological, psychological, and behavioural parameters of the organisms in ways that increase its capacity and tendency to respond adaptively to the threats and opportunities characteristic of specific kinds of situations”*. This is in line with Darwin's (1872) earliest work, reported in the book *“The Expression of the Emotions in Man and Animal”*, where he proposes that emotions serve as communicative signals used by both animals and humans for adaptive purposes and that facial expressions of emotions represent innate and automatic behaviour patterns, crucial component of human emotional and social behaviour. This renders emotions and their facial expression not only salient social stimuli but also evolutionarily relevant stimuli. Humans have evolved to live within groups and engage in complex social interactions and facial expressions of emotions facilitate the understanding of other's moods and intentions as well as the regulation of responses adapted to these perceived moods and intentions. Thus, emotional signals induce action tendencies in the observer, in the same way as surrounding objects provide action possibilities (McArthur & Baron, 1983). For instance unexpectedly facing a threatening agent, such as an angry individual, would be expected to

induce withdrawal tendencies and preparation of avoidance responses in the observer. These action tendencies essentially determine the functional significance of the emotion and vice versa, linking perception and action (Blair, 2003; Compton, 2003; Gaigg, 2012). Emotions can be defined by their particular communicative role which in turn impacts on the perception of the emotion itself; not only emotions induce action tendencies in the observer, but also the specific action tendencies influence the way in which the emotion or its social function will be perceived. Thus, the ability to respond in a socially adaptive way depends not only on the accurate perception of another's social signals but also on the accurate evaluation of the meaning of these signals for the observer. All of the above are critical for successful online social interaction, which is a continuous reciprocal process, and they, subsequently, render the face as a source of highly important, socially relevant information.

Thus, the ability to decode facial expressions of emotion plays a fundamental role in the modification and adaptation of appropriate social behaviours, which makes it an important component of successful social functioning. Emotion knowledge, which refers to the ability to understand emotion from facial expressions, behavioural cues, and social contexts develops early in life and contributes to future abilities in managing and responding to emotions (Izard, 1971). In typical development, infants as young as 7 months old can accurately discriminate between emotional expressions (Leppänen, Moulson, Vogel-farley, & Nelson, 2007) and this ability develops through childhood to adolescence, when children become emotion recognition experts (Herba & Phillips, 2004). Social competence is a key correlate of emotion perception and understanding across childhood to adolescence (Trentacosta & Fine, 2010). TD children with low social skills perform worse in emotion decoding tasks as compared to children with relatively better social skills (Custrini & Feldman, 1989; Philippot & Feldman, 1990). Individuals with ASD are characterised by reduced social competence in comparison to their peers (Catherine Lord, 1993), which increases with age as social demands themselves increase. A vast part of the literature stresses that ASD is characterised by poor emotion understanding. Thus, it is important to study face perception and importantly, facial affect understanding in psychiatric populations such as ASD. This might shed light not only to what underlines the persistent social deficits that characterise individuals with ASD but also to the link between social and affective competences in both ASD and typical development.

1.3 Processing of facial expressions of emotion in autism spectrum disorders

As explained in the previous sections the first step for emotion understanding is the capacity for accurate decoding and processing of emotional signals from the face. Failure to process emotional signals would have profound consequences on the individuals learning of other's emotions and responses. Thus it has been suggested that decoding and processing facial expressions of emotions might be deficient in ASD. The literature, however, is vast and the findings are inconsistent. In this section I will provide a literature review of the research findings in emotion processing abilities in children and adolescents with ASD, because the focus of this Ph.D. is on adolescents aged between 12 and 17 years old. Given that the literature review is organised in terms of the methodological factors that influence these findings, the age group selection will be justified at the end of the literature review, in section 1.3.5.

1.3.1 Early studies on emotion processing in children and adolescents

The most dominant account supports that individuals with ASD are characterised by a generalised, fundamental deficit in emotion understanding and processing (Davies, Dapretto, Sigman, Sepeta, & Bookheimer, 2011; Gaigg, 2012; Harms, Martin, & Wallace, 2010) and reduced activation of emotion related brain areas in comparison to TD controls such as the fusiform gyrus and the amygdala (Corbett et al., 2009; Loveland, Bachevalier, & Lane, 2008). However, both groups have been found to perform similarly in well-controlled studies when the ASD group is matched with controls according to intelligence quotient (IQ) and mental age for example (Blair, 2003; C. R. G. Jones et al., 2011; Ozonoff, Pennington, & Rogers, 1990) or when the emotion strength of the stimuli is 100% (Gaigg, 2012). A relatively recent meta-analysis of the literature on emotion recognition abilities in ASD (Uljarevic & Hamilton, 2013) looked at 48 studies including approximately 950 participants with ASD and found a large publication bias. After controlling for it the original effect size of the emotion recognition difficulties in ASD as compared to TD was reduced to half (from 0.80 to 0.41) but it was still significantly different from zero. This suggests that indeed an emotion decoding difficulty might exist in ASD but the magnitude of it is not close to what was initially thought. In this section I will review the evidence for and against an overall emotion processing impairment in ASD.

Early studies pointed to a generalised emotion decoding deficit in ASD. Hobson, (1986a, 1986b) investigated the matching of objects, schematic and real facial expressions of emotions to videotaped gestures, vocalisation and contexts and vice versa, in ASD children as compared to several control groups. Although, ASD children were equally good as control groups in matching non-social objects to the presented cues, they were significantly worse than both TD individuals and non-ASD individuals with intellectual disabilities (ID), at matching facial expressions of emotion with videotaped cues (see

Figure 1, for an example of schematic stimuli).

They were significantly worse than non-ASD children with ID when matching gestures to videotaped facial expressions of emotions suggesting a difficulty in this group to identify the correspondence between emotional information and facial expressions of emotion (Hobson, 1986b). Similarly, when asked to sort pairs of photos depicting people who differed in one or more of four variables, these being their age, sex, their hat and their facial expression of emotion, children with ASD prioritised the sorting according to the type of hat (Weeks & Hobson, 1987), while the majority of non-ASD children sorted the photographs according to the facial expression of the individual. According to the authors these results reflect enhanced saliency of facial expressions in non-ASD populations, but insensitivity to others' facial expressions of emotion in ASD. Moreover, adolescents and

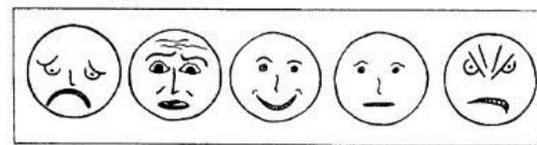
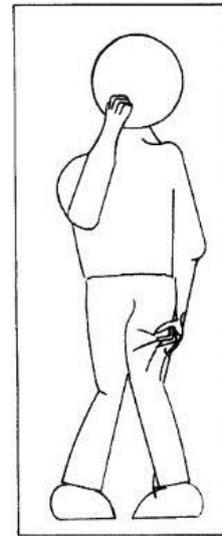


Figure 1: Example of a fearful stimulus from Hobson et al., (1986a). Participants were given schematic postures (upper panel) and were asked to choose a facial expression of the bottom panel to “go with” the schematic posture.

adults with ASD were worse in matching facial expressions of emotions to emotional vocalisations as compared to non-ASD controls with ID while there was no significant difference when matching non-emotional images to recorded sounds (Hobson, Ouston, & Lee, 1988). Similar deficits were found in children with ASD as compared to a group of ID, specifically Down syndrome, and to a TD group when they were asked to match stimuli on the basis of emotion or identity (Celani, Battacchi, & Arcidiacono, 1999). Impairments specific to matching affect, faces, or affect to context (written situations) were also found in children with pervasive developmental disorders² (PDD), although such deficits were not evident when the participants were asked to match objects (Braverman, Fein, Lucci, & Waterhouse, 1989; Fein, Lucci, Braverman, & Waterhouse, 1992). However, Braverman et al., (1989) reported that the size of the difference between groups was surprisingly small (see Figure 2) especially as compared to previous findings by Hobson and colleagues (1986; Weeks & Hobson, 1987), which implies that they considered the difference statistically, but not practically, significant.

² PDD referred to a set of developmental disorders characterised by communicative and socialisation deficits. These included PDD not otherwise specified (PDD-NOS – infantile autism), Asperger’s Syndrome, autism, Rett syndrome and childhood disintegrative disorder (CDD). Since the DSM-V PDD has been integrated in ASD.

A Table I. Test Scores of Pervasive Developmental Disorders Versus Matched Normal Controls

	PDD (<i>n</i> = 15)		DAD matched controls (<i>n</i> = 15)		Peabody matched controls (<i>n</i> = 15)	
	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>
Objects	11.60	2.69	11.60	2.77	11.60	2.16
Faces	10.20	3.36	12.00	3.07	10.80	2.11
Affects	9.67	2.89	12.47 ^a	3.66	11.00	3.25
Affect comprehension	11.07	3.28	13.87 ^a	2.29	12.93	2.68
Affect labeling	13.00	2.93	14.40	2.38	14.33	2.06

^a*p* < .05, difference from PDD.

B Table II. Test Scores of Autistic Versus Matched Normal Controls

	Autistic (<i>n</i> = 10)		DAD matched controls (<i>n</i> = 10)		Peabody matched controls (<i>n</i> = 10)	
	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>
Objects	11.80	3.11	11.90	3.11	11.00	2.16
Faces	9.60	3.47	12.20	3.45	10.40	2.27
Affects	9.00	2.94	13.30 ^a	3.20	10.70	2.50
Affect comprehension	10.50	2.99	14.30 ^a	2.16	12.00	2.78
Affect labeling	13.00	2.66	15.10 ^a	1.28	13.90	2.28

^a*p* < .05, difference from PDD.

Figure 2 : from Braverman et al., (1989). Between groups for A) the whole ASD group and B) the subgroup which showed greatest autistic deficits. Draw-a-Design (DAD) refers to the control group matched with the ASD group on non-verbal mental age and Peabody refers to the control group matched with the ASD group on the Peabody Picture Vocabulary test (Dunn & Dunn, 2007) which is a verbal mental age measure. Conditions revealing group differences are noted in red.

Over the years a number of studies, the majority in adults, followed with different paradigms, using a variety of different stimuli, of varied difficulty attempting to identify whether there is a fundamental deficit in emotion processing in ASD but the results remain highly inconsistent with approximately one in four of these studies failing to show atypical emotional processing in ASD (for comprehensive reviews see Gaigg, 2012 and Harms et al., 2010). In a recent matching paradigm (Begeer, Rieffe, Terwogt, & Stockmann, 2006), ASD children did not spontaneously choose the facial expression of emotion depicted in the cards as the sorting criterion to categorise them, replicating previous findings of Weeks & Hobson, (1987). More recently, Jones et al., (2011) tested 99 adolescents with ASD on multimodal emotion recognition, involving a facial affect recognition task and found no differences between adolescents with ASD and controls. Moreover, they analysed the error patterns and did not find group differences suggesting that ASD adolescents were equally confused with TD controls when judging an emotional expression. These are indicative examples of recent studies in children that found (Baron-cohen, Spitz, & Cross, 1993; Kuusikko et al., 2009; Luckhardt, Kröger,

Cholemkery, Bender, & Freitag, 2017) or not (Back, Ropar, & Mitchell, 2007; Buitelaar, van der Wees, Swaab-Barneveld, & van der Gaag, 1999; Castelli, 2005) group differences in the processing of facial affect and which suggest that over the years the findings remained equally inconsistent.

A key finding comes from a study by Wright et al., (2008) who investigated emotion decoding in children and adolescents with ASD. They found that the diagnosis of ASD accounted only for 1% of the variance between the two groups in emotion recognition while age, gender and IQ accounted for an additional 55% of the same variance (see Figure 3). It is proposed that methodological details, such as the age, matching variables (IQ) and the control groups used should be addressed when considering the evidence for and against a fundamental deficit in emotion processing in ASD. This would have important implications for individuals with ASD given that, especially those on the milder end of the spectrum, are able to process emotions not only in an experimental setting but also in real life (Harms et al., 2010).

	Happiness	Sadness	Anger	Fear	Surprise	Disgust	Total
<i>Block 1 (age, sex, IQ score)</i>							
<i>R²</i>	0.17	0.16	0.30	0.25	0.35	0.35	0.55
<i>p</i>	(0.006)	(0.009)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)
<i>Block 2 (block 1 + diagnosis)</i>							
<i>R²</i>	0.22	0.17	0.36	0.25	0.36	0.36	0.56
<i>p</i>	(0.003)	(0.016)	(<0.001)	(0.001)	(<0.001)	(<0.001)	(<0.001)
<i>ΔR²</i>	0.05	0.01	0.06	0.00	0.01	0.01	0.00
<i>Δp</i>	(0.045)	(0.381)	(0.015)	(0.877)	(0.122)	(0.431)	(0.464)

Figure 3 : Hierarchical regression analyses showing the variance accounted for by the effects of age, gender (sex), IQ score and diagnosis on emotional recognition. Table from Wright et al., (2008). The parameters of interest here are noted in red.

1.3.2 Matching and control group selection

Several studies that match the groups carefully on verbal mental age find no differences in emotion decoding in children and young adolescents with ASD. In the Braverman et al., (1989) for example when the ASD group was compared to the Peabody control group, which was matched on verbal mental age, there were no significant differences in performance (refer to Figure 2). Additionally, Ozonoff et al., (1990) used an emotion and identity sorting task across two experiments which included the same but 3 ASD participants, in order to investigate the emotion perception deficits under different matching conditions. When they matched individuals on verbal mental age in the first experiment they found no differences between the ASD group and the TD group. However, when the same ASD kids were matched with a TD group on nonverbal mental age the affect matching deficits mentioned above arose. ASD children are considerably better in non-verbal tasks than on verbal ones, suggesting that matching

them on the non-verbal aspect would lead to comparing them with TD children who are older in regard to their mental age. Similarly, the deficits found in Braverman et al., (1989) and Fein et al., (1992) disappeared when the researchers matched their groups on verbal mental age and deficits found in the ASD group in the Hobson, (1986b) matching task disappeared when the groups were matched on verbal mental age (Prior, Dahlstrom, & Squires, 1990). Castelli, (2005) investigated the recognition and naming of facial expressions of basic emotions (Ekman, 1999) - anger, fear, disgust, happiness, sadness and surprise – of natural and different intensities. The TD and ASD groups were matched on verbal IQ and they were comparable not only in their recognition of facial expressions of different intensities but also

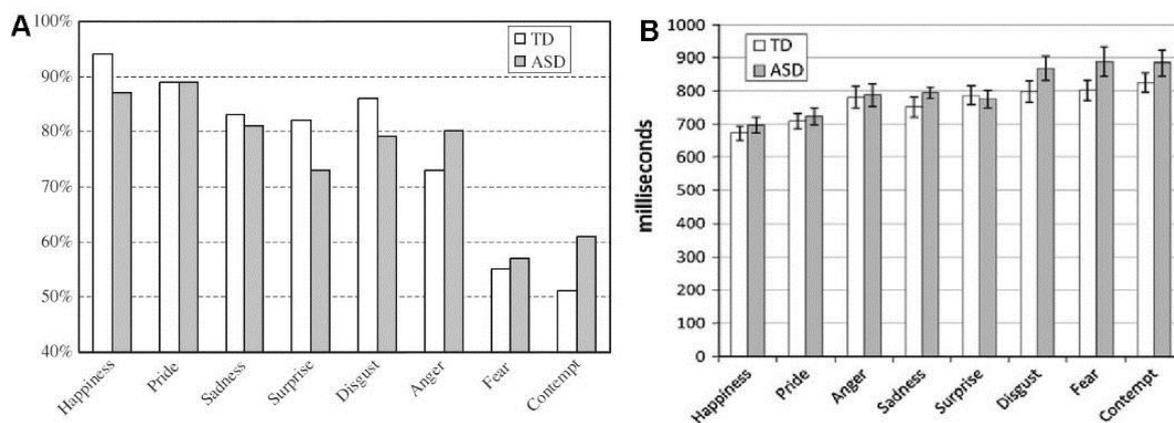


Figure 4: Results from Tracy et al., (2011). A) Accuracy results (%). B) Reaction times results (ms). Note that there were no significant differences between the groups for neither variables.

on the naming of emotion with natural, prototypic (100%) intensity.

Moreover, differences in facial emotion recognition are less prevalent across a range of tasks when the groups are matched on full scale IQ. Both Rosset et al., (2008) and Grossman, Klin, Carter, & Volkmar, (2000) who matched their TD and ASD on verbal and full scale IQ found no differences in the recognition of basic emotions. A recent study matched the groups on verbal, performance and full scale IQ and tested emotion recognition using a block design, with each block assessing an emotion (different each time) between other distractor emotions (Tracy, Robins, Schriber, & Solomon, 2011). No group differences were found between groups either in emotion recognition (Figure 4A) or in reaction times (RTs; Figure 4B). Importantly, for both groups recognition of all emotions was significantly greater than chance except for the emotions of fear and contempt, but this is not surprising given that these emotions elicit significantly lower decoding rates than other emotions in typical individuals across cultures (Elfenbein & Ambady, 2002). In another study, low and high functioning children and adolescents with ASD demonstrated intact emotion decoding in response to dynamic stimuli, which included verbal and nonverbal affect and this affect was either implicit or explicit (Figure 5). There were no differences in comparison to low and high functioning TD groups accordingly, although only the high

functioning group in this study was matched for both verbal and nonverbal IQ (Loveland, 1997). Differences were found when participants were grouped into high and low functioning, with the high functioning relying mostly on nonverbal information in cases where the emotion was not explicitly stated. In another study, there were no overall emotion recognition differences between young ASD and TD children that were matched for developmental level, in response to dynamic or still stimuli (Gepner, Deruelle, & Grynfelett, 2001). The findings are not surprising given that emotion perception abilities in ASD are largely related to age (Harms et al., 2010) and most importantly IQ, with high IQ adolescents with ASD performing better at recognising emotions than lower IQ ones (Jones et al., 2011).

Condition	Verbal Information for Affect Present?	Nonverbal Information for Affect Present?	Example
Explicit/animate	Yes	Yes	“I’m happy because I’m going to the zoo” with happy face and voice
Explicit/flat	Yes	No	“An elephant was in the elevator. Boy, what a surprise” with flat face and voice
Implicit/animate	Yes, but implied	Yes	“My roommate borrowed my books and now he’s lost them” with angry face and voice
Implicit/flat	Yes, but implied	No	“It’s my birthday today, and I got some wonderful presents” with flat face and voice
Neutral/animate	No	Yes	“Today is Thursday, and I will go to school” with angry face and voice
Neutral/flat	No	No	“My father takes an umbrella to work with him when it rains” with flat face and voice

Figure 5 : Experimental conditions in the study by Loveland, (1997).

When discussing the matching variables it is useful to consider the choice of the control group, and specifically their cognitive profile. This plays an important role in the observed differences between groups and particularly when low functioning children or adolescents with ASD are concerned. As we saw at the start of the section 1.3 many studies that found failures in emotion processing in ASD matched their group with ID control groups according only to their chronological age. Most studies that use ID control groups use either a group of individuals with Down syndrome or with unknown aetiologies. It is important to note that ID and deficits in processing of facial affect are highly associated, as the evidence reviewed above also confirms. Individuals with conditions like Down syndrome are impaired in the processing of fearful facial expressions (Wishart, 2007). When ASD children are compared to ID control groups they present both intact (Loveland, 1997) and deficient (Celani et al., 1999) processing. The reason for the above could lie on the association of the choice of matching variable and the choice of the control group. For instance, when the ASD group was matched according to verbal mental age with a younger in terms of chronological age TD control group no emotion perception deficits were found (Braverman et al., 1989). These results implicate

methodological factors, such as the choice of the control group and the matching variables, in the likelihood of finding group differences between ASD and TD individuals in the perception of facial affect.

1.3.3 Type of stimuli

The performance of ASD individuals in processing facial affect depends on several other methodological factors and importantly on the type of stimuli used in each study. Rosset et al., (2008) investigated the processing of emotional expressions of real faces, human cartoon faces and non-human cartoon faces in young children with ASD (Figure 6). Participants saw happy, sad and angry stimuli of each condition in both upright and inverted orientations and were asked to categorise them. Importantly, the ASD group was matched to two TD groups, one according to chronological age and to the other according to mental age. There were no differences between the groups in overall accuracy in emotion categorisation, regardless of which control group was used. However, while TD children showed an inversion effect, characterised by reduced accuracy in emotion categorisation in the inverse condition for human faces, the ASD group showed the same effect for human and non-human cartoon faces but not for real human faces. In another study (Brosnan, Johnson, Grawmeyer, Chapman, & Benton, 2015), two groups of TD adolescents showed an advantage in emotion decoding of human faces over a group of 37 adolescents with ASD, but when animated faces were used there were no differences between the groups for neither dynamic or static stimuli. Specifically, when static or animated stimuli were used the ASD group outperformed the TD group. Similarly, using static, human face stimuli another study (Buitelaar et al., 1999) demonstrated accurate emotion processing of complex and basic emotions. Participants were firstly asked to match facial expressions of emotions and secondly to categorise emotionally loaded situations, which included an individual without a facial expression, according to the emotion that they thought was represented in the situation. The ASD groups' performance was comparable to the controls.

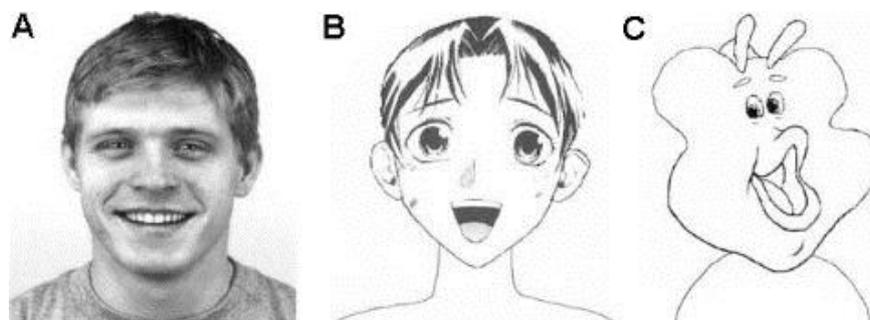


Figure 6 : Examples of happy stimuli used in emotion categorisation, from Rosset et al., (2008).
A) Human face. B) Human cartoon face. C) Non-human cartoon face.

Overall, individuals with ASD are better in response to static stimuli but their performance in emotion decoding depends also on the intensity of the faces. Children with ASD recognised facial expressions of anger, sadness, fear, happiness and disgust equally well and as quickly as TD and social phobia comparison groups and showed the same speed (happiness<anger, disgust; sad<fear) and accuracy advantage (happy>disgust) for specific emotions over others (Wong, Beidel, Sarver, & Sims, 2012). However, between groups differences were found in relation to the intensity of the facial expressions. ASD children were less accurate in the detection of low intensity expressions than TD children. In another study using dynamic stimuli (Law Smith, Montagne, Perrett, Gill, & Gallagher, 2010) adolescents with ASD were worse at decoding facial expressions of disgust, anger and surprise (see Figure 7A), but for anger and surprise recognition was impaired only at low levels of intensity and not at full blown (100%; see Figure 7B). There were no differences in the RT results between groups and the authors, in contrast with previous studies, suggests that the ASD group might not use different mechanisms or strategies to solve the task. Comparable RTs between the groups, as they propose, suggest that they could detect subtle, low-level perceptual differences but might have failed to discriminate the emotions at those levels.

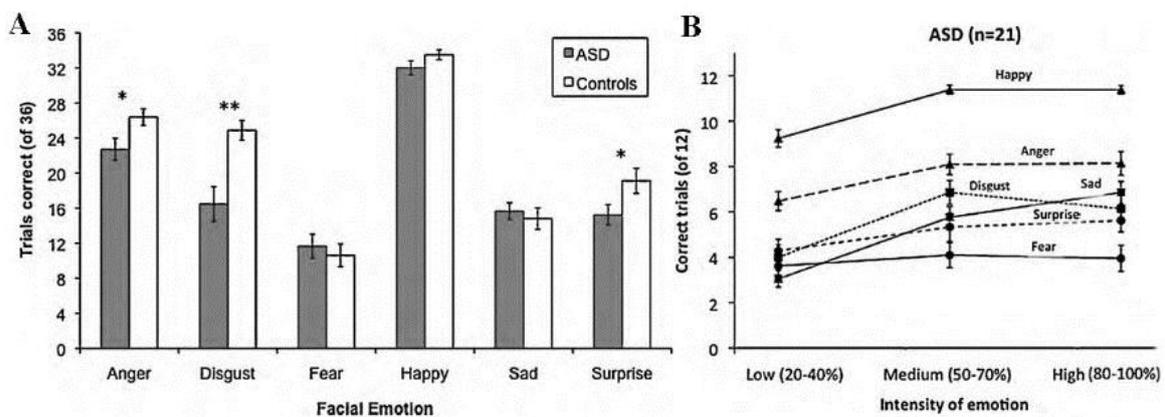


Figure 7 : from Law Smith et al., (2010): A) Emotion categorisation performance for both ASD and TD groups. The ASD group performed worse than the TD group in the decoding of anger, surprise and disgust. B) The differences between groups in the recognition of anger and surprise were specific to low and medium intensities. For high intensities they performed like controls.

1.3.4 Eye-region fixation

In sections 1.1 and 1.2, I stressed the general inattention and absence of spontaneous orientation towards salient social stimuli in ASD, such as the eye-region of the interlocutor. This has been reported in the literature from the first definitions of autism, is found in young children with ASD and in this section I will explain how it influences participants' performance.

A failure to engage in appropriate eye-contact and an indifference to the faces of others are characteristic of ASD from the first description of their symptomatology (Kanner, 1943) and reduced attention to others' eyes is evident from approximately 2-6 months of age in infants who are later diagnosed with ASD (Jones & Klin, 2013). Individuals with ASD present reduced or deviant fixation patterns to the eyes of others (Corden, Chilvers, & Skuse, 2008; Pelphrey et al., 2002; Senju & Johnson, 2009; Spezio, Adolphs, Hurley, & Piven, 2007) and enhanced attention to the mouth region instead (Klin, Jones, Schultz, Volkmar, & Cohen, 2002). Spezio, Adolphs, Hurley, & Piven, (2007) used the "Bubbles" technique to occlude different areas of the same face in order to create different stimuli and then assessed which information each of the two different groups use when they judge emotions from the face accurately. They found that while the TD group used information from the eyes, the ASD group used information from the mouth. Similarly, Grossman & Tager-Flusberg, (2008) assessed the ability of adolescents with and without autism to implicitly process facial expressions of emotions or lip-read words mimed by the same stimuli, both when the eyes of the stimuli were masked and unmasked. The TD group performed better in the emotion task and worse in the word task in the unmasked condition, when they could extract information from the eyes. However, emotion accuracy of the ASD group was comparable across the masked and unmasked conditions (see Figure 8) suggesting that collection of information from the eyes is not prioritised in this group.

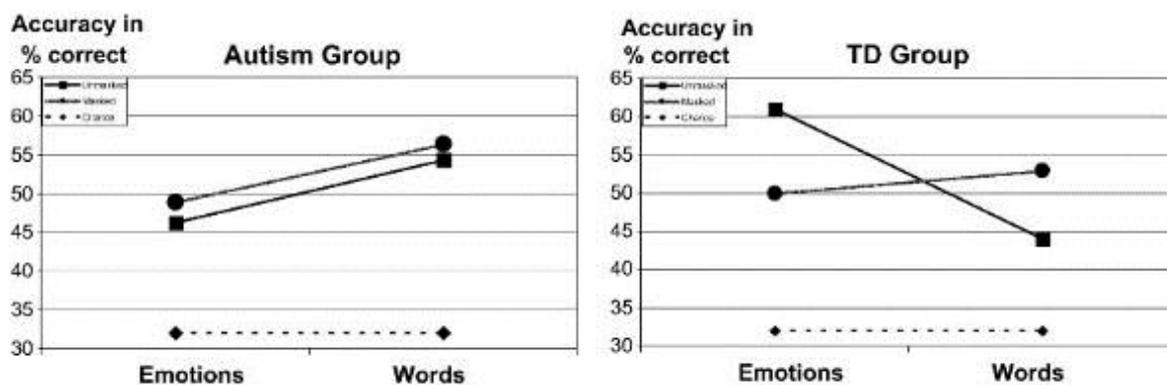


Figure 8 : Performance of the ASD (left) and TD (right) groups in both the masked (bullet) and unmasked (square) conditions from Grossman & Tager-Flusberg, (2008). The bottom dot line represents the chance level.

At the same time there is a part of the literature that presents doubts regarding the deviant social attention or gaze in ASD. Some report no group differences at all while others report differences only in areas of the face that surround specifically the eyes, in experimental conditions which are complex, i.e. gaze following (Fletcher-Watson, Leekam, Benson, Frank, & Findlay, 2009; Freeth, Chapman, Ropar, & Mitchell, 2010). Recently an exhaustive study with a large sample size (N = 81) disentangled this by investigating social attention of individuals with ASD using three different visual exploration paradigms; one static, one dynamic or one interactive (Chevallier et al., 2015). The total

time spent fixating to the eye-region of others depended on the task for the ASD group and meaningful group differences appeared when tasks became interactive and thus more ecological, suggesting that reduced social attention is indeed characteristic of this group at least in the most realistic, ecologically valid paradigms, in which we are most interested. This is in line with past findings in ASD that favour a failure to adjust one's level of attention to social stimuli as a function of the stimulus' changes in saliency (Birmingham, Cerf, & Adolphs, 2011; Horlin et al., 2013). Importantly, total fixation duration is positively correlated with the activation of the fusiform gyrus and the amygdala in response to faces (Dalton et al., 2005). Hypoactivation of FG and hyperactivation of the amygdala has been widely reported in ASD in response to threatening social and emotional cues and the authors proposed that the variation in eye-region fixation could account for this variation in activity in response to faces (Dalton et al., 2005). This suggests reduced responses to faces and heightened emotional responses to gaze fixations in ASD. These findings put forward three suggestions: 1) individuals with ASD do not find mutual gaze pleasant, 2) their gaze fixation duration pattern is associated with their ability to process faces and 3) there are no deficits in the ability to orient to these features but rather deficits in the spontaneity or prioritisation of this orientation. Similarly a lack of spontaneity/prioritisation to engage in social interaction or social tasks, rather than an inability to perform the tasks themselves, could underlie observed behavioural deficits in ASD.

In the mimicry literature, individuals with ASD showed reduced spontaneous facial mimicry in response to happy and angry facial expressions but when asked to voluntarily mimic the expression of others they do so successfully (McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006), suggesting that there is mimicking ability in ASD but its automaticity is deficient. Similarly, in a study by Begeer et al., (2006) the ASD group failed to match cards according to their emotional expression only when the matching was implicit and they could choose amongst 3 matching criteria; presence of glasses, presence of moustache and emotional expression. The ASD group spontaneously chose non-social and non-emotional criteria. When however, they were explicitly asked to match the cards according to the emotion all group differences disappeared, suggesting that the abilities are intact but the salience of emotions or their prioritisation might be reduced. Given that this *impaired* performance is underlined by intact abilities and manifests due to a lack of spontaneous engagement with the social world, then lack of spontaneous orientation specifically to the eye-region would be expected to lead to similar results (impaired performance) in tasks assessing abilities which are however preserved. In cases like these, explicit instruction or use of jitters to direct attention to relevant cues of the social world, in this case the eye-region, should lead to typical performance of the ASD group. In support of that individuals with ASD do not show contagious yawning in response to someone else yawning, which is considered mimicry, but when children with ASD were asked to fixate the eyes of the face stimuli, they

yawned equally frequently to the TD group (Senju et al., 2009). In a different study (Rutherford & Krysko, 2008) measuring reflexive attentional shifts in response to gaze direction or head movement direction changes, participants were asked to focus on the fixation point and indicate the location of a target point that would appear and disappear, while ignoring any face images that appeared concomitantly. Following instruction to attend to the fixation cross, and in the absence of a social task (ignore faces), the ASD and TD groups performed similarly, so that the salient social cues, in this case gaze direction change, influenced both groups more than the head movement (see Figure 9). We could argue the possibility that the same is the case in emotion recognition tasks, where ASD participants would fail because they do not spontaneously orient to the eyes, rather than because of an inability to perceive emotions.

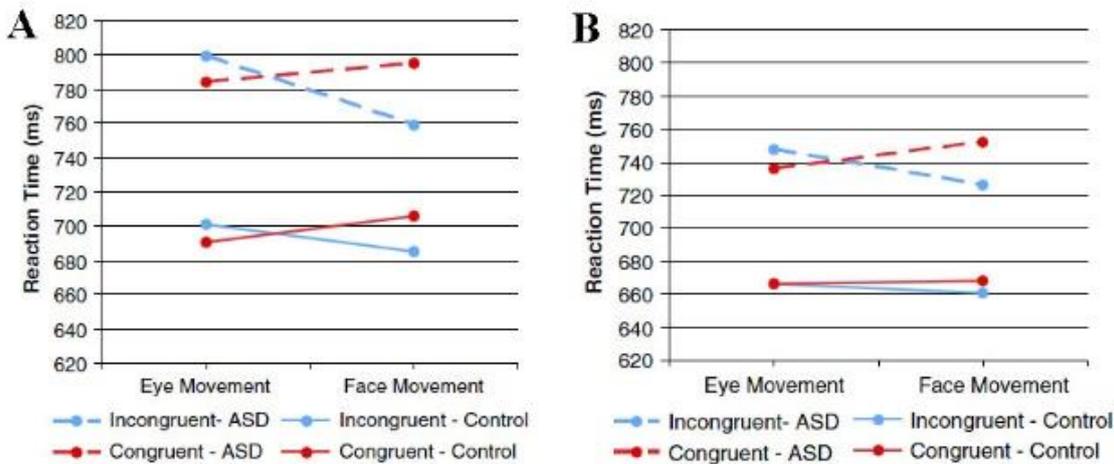


Figure 9: Results from Rutherford & Krysko, (2008) for A) 100ms and B) 800ms stimulus presentation during target appearance. The gaze direction or head movement were either congruent or incongruent with the side in which the target appeared.

In support of this argument, firstly, emotion recognition abilities depend on one’s capacity to focus on relevant information (Kuusikko et al., 2009), secondly attention to eye-region is linked to emotion decoding performance (Bal et al., 2010) and thirdly, eye-tracking findings suggest that people who orient spontaneously to others’ eyes, show greater emotion recognition abilities (Kirchner, Hatri, Heekeren, & Dziobek, 2011). This is particularly important for threatening emotions, such as fear and anger given that these emotions are predominantly expressed in the upper part of the face (Dimberg & Petterson, 2000). Thus individuals with ASD might not decode emotions accurately because they do not spontaneously look at the appropriate features of the face. Specifically in ASD, which is characterised by deviant gaze behaviour, this is highly relevant because the group’s fixation time on the eyes or mouth of the stimulus predicts their emotion recognition performance (see Figure 10 from Kirchner, Hatri, Heekeren, & Dziobek, 2011). Hence, the absence of methodological implementations to intentionally

allocate the participants' attention to relevant social cues could bring individuals with ASD at a disadvantage as compared to their age-matched controls (Chevallier, Kohls, et al., 2012).

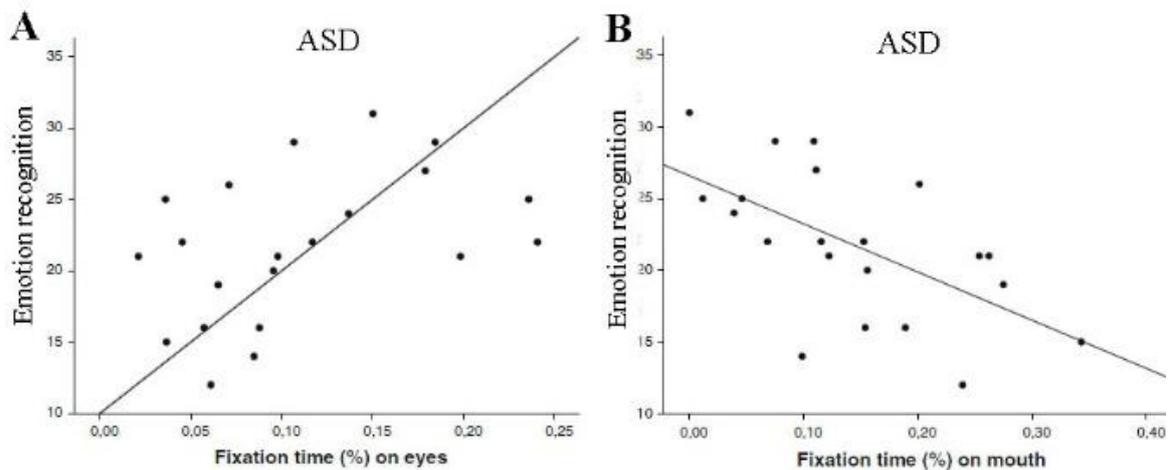


Figure 10 : from Kirchner et al., (2011). A) Fixation on the eye-region is a positive predictor of emotion recognition performance in the ASD group and B) fixation to the mouth is a negative predictor of emotion recognition performance in ASD.

1.3.5 Age, why adolescents?

In the above literature review I focused on emotion processing abilities in children and adolescents with ASD and I presented the most prominent methodological factors that influence their performance. In children emotion processing is mostly assessed using static, high intensity stimuli and the results are based on the recognition accuracy. In adolescents, as we saw the tasks are more refined with different emotion strengths and extra variables such as RTs but still mixed results are reported in adolescent groups. The results in adults, using a variety of different methodologies and variables of interest, are similar (for a comprehensive review see Harms et al., 2010): while some find no group differences when high-functioning adult ASD groups are compared to neurotypical controls (Adolphs, Sears, & Piven, 2001; Rutherford & Towns, 2008), others find that they are deficient in recognising emotions and particularly negative ones (Ashwin, Baron-Cohen, Wheelwright, O’Riordan, & Bullmore, 2007; Corden et al., 2008; Philip et al., 2010; Wallace et al., 2011). In this doctoral work we are interested in development and specifically in perception of threat in adolescents with ASD between the ages of 12 and 17 years old, rather than in children. But why is that?

Firstly, although emotion abilities increase with age, children become experts and can achieve adult levels of emotion interpretation around the age of 11 years old (Custrini & Feldman, 1989; Tonks, Williams, Frampton, Yates, & Slater, 2007). Studies investigating emotions abilities in ASD groups have found that younger children can present intact decoding of pure expressions of emotions, however, when compared to adolescents they might be impaired (Kuusikko et al., 2009). Such age group

differences in emotion processing become even more prominent when complex and ambiguous expressions are involved, i.e. ones resulting from blending different emotions (Kuusikko et al., 2009). Thus, investigating adolescents allows for more complex expressions to be used. This means that not only blended but also ambiguous facial expressions of threat can be used, which are more ecological, given that in everyday life people rarely express full intensity emotions. In line with this, investigation of children's emotion abilities is limited to the analysis of emotion recognition accuracy because tasks have to be simpler (see section 1.3). Working with adolescents, on the other hand, allows for more complex tasks to be used and more variables of interest, such as RTs and physiological measures (eye-tracking, mouse-tacking).

Secondly, in typical development emotion decoding abilities improve with age from childhood throughout adolescence (Thomas, Bellis, Graham, & LaBar, 2007; Vicari, Reilly, Pasqualetti, Vizzotto, & Caltagirone, 2000) in a continuous fashion (Herba & Phillips, 2004). Evidence from neurodevelopmental studies suggests that brain areas responsible for the processing of facial expression of emotion develop throughout late childhood and adolescence, when they start showing corresponding functional differences. The amygdala and the fusiform gyrus for example continue to develop throughout adolescence (Aylward et al., 2005; Schumann et al., 2004; Thomas et al., 2001) and the prefrontal cortex (PFC) is of the last areas to mature (Casey, Giedd, & Thomas, 2000; Casey, Tottenham, Liston, & Durston, 2005). This is highly relevant for the study of emotions and particularly threat in ASD because the amygdala for example is a core area for guiding the individual's attention to social, biologically relevant stimuli. The amygdala guides attention to the eyes, faces or biological motion (Adolphs & Spezio, 2006) and might be responsible for computing and updating the value of social orienting (Klein, Shepherd, & Platt, 2009). Moreover, it is implicated in the understanding of the significance of information of the face, such as emotions (Aylward et al., 2005) and specifically threatening ones (Adolphs, 2008), which are predominantly expressed using the upper part of the face (Fridlund, 1997). ASD has been characterised by abnormal activation of the amygdala (Hadjikhani, Joseph, Snyder, & Tager-Flusberg, 2007) as compared to TD individuals and by differences in amygdala volume and activation. Importantly, differences are observed between age groups within the ASD group. ASD children have enlarged amygdala volume in comparison to TD children but adolescents with ASD aged 12 to 18 years old do not differ from TD adolescents in amygdala volume (Schumann et al., 2004), and thus allow for better controlled comparisons between groups.

Most importantly, the social brain, which refers to the network behind understanding and interacting with others, undergoes big changes during early adolescence, as individuals show enhanced desire to socialise with others but social exchanges begin to require more sophisticated skills (Howlin, 2003). This is a critical period for the transition from childhood to adulthood with age-specific social,

psychological and physical characteristics which are thought to promote independence (Spear, 2000). Neural connections are being remodelled in comparison to childhood because of the PFC development during early adolescence (≈ 10 years old) with changes in not only goal directed behaviours but also in emotion processing of aversive stimuli (Spear, 2000). This is highly relevant to the present thesis that uses aversive stimuli and focuses on the processing of social threats. Importantly, adolescents offer a better case for studying emotion processing as compared to adults because they show greater connectivity between prefrontal areas (Burnett & Blakemore, 2009), they are more sensitive to emotional ambiguity (Thomas et al., 2001), their frontal activity is modulated by the emotional nature of the stimulus rather than by its attentional demands – which is the case in adulthood - (Blakemore, 2008; Christopher S. Monk et al., 2003) and they show enhanced neural reactivity in response to social threats (Hare et al., 2008). The latter is the case not only in comparison to adults but also to children. Lastly, there are not many symptom improvements related to reciprocal social interaction between adolescence and adulthood in ASD when improvements happen only in the domains of repetitive and restrictive interests (Seltzer, Shattuck, Abbeduto, & Greenberg, 2004).

It appears that age is an important determinant of emotion abilities and adolescence is a developmental period distinct from childhood and adulthood, which allows for more refined and detailed investigation of emotion abilities in typical development and in ASD. Thus, the focus of this doctoral work will be on the perception of threatening emotions in adolescents with ASD.

Section 1.3 conclusion

In the start of this section I presented you with the most dominant account in the literature, proposing a fundamental, generalised deficit in emotion processing in ASD. However, the findings in the literature are mixed and the performance of the ASD group depends on methodological and demographic factors. Such factors include the matched control group, the variables of matching, the age of the participants and so on, all of which contribute to the heterogeneity of findings regarding processing of facial affect in ASD. Moreover, it is important to note that most studies investigated the processing of one facial social cue at a time, which cannot give a full picture of the processing abilities in this group. In real life situations an emotional expression is never presented alone but it is always in context, which might affect and in some cases even enhance the processing of the emotion. The contextual influences on emotion processing in neurotypical individuals and individuals with ASD will be discussed in depth in Chapter 2 where the first experiment of this Ph.D. will be introduced, and emotion processing in adolescents with ASD will be investigated.

Given the above, although we cannot claim that individuals with ASD process facial affect in an entirely typical fashion, we can argue that a fundamental deficit in processing of facial expressions of emotion in ASD seems unlikely. When evaluating the nature of a deficit which is proposed to be

fundamental in a condition, some criteria need to be fulfilled (Ozonoff et al., 1990). Firstly, the deficit needs to be universally specific to the condition and distinguish ASD from any other clinical groups. As we saw above, emotion processing deficits can also be found in individuals with lower verbal intelligence, such as Down syndrome. Secondly, it should persist and impair features of the disorder and thirdly, it should be the fundamental deficit behind these impaired features of the disorder. If an emotion processing deficit was fundamental in ASD then it should persist across paradigms, stimuli and comparison groups, be specific to the condition and independent of developmental factors. However, the review of literature above points to the opposite direction rendering the suggestion of a fundamental emotion processing deficit in ASD unconvincing. In the next section I will present two recent relevant theoretical frameworks for the processing of facial affect and specifically threat in ASD, which attempt to provide answers in regard to the emotion processing abilities of this group.

1.4 Relevant theoretical frameworks

Recently, two relatively new theoretical frameworks have become particularly relevant to the research investigating affective difficulties in individuals with ASD. Both frameworks focus on atypicalities in processes which are domain specific and operate mainly, or even solely, during social interactions (Gaigg, 2012). The first one includes behavioural self-regulation accounts (Bachevalier & Loveland, 2006; K. A. Loveland, 2005; K Loveland, 2001) and posits that given the intimate action-perception link, it is not only the processing of facial expressions of emotion that could be deficient in ASD but also that the mechanism behind the regulation of appropriate responses might be too. The second framework includes social motivation accounts (Chevallier, Kohls, et al., 2012; Dawson et al., 2005; Grelotti et al., 2002) which stem from evidence of atypical attention and orientation to faces in ASD. According to this theory, atypicalities in emotion recognition would rather result from an overall lack of motivation to attend to relevant socio-emotional stimuli, rather than from a failure in the mechanisms *per se*. In this section I will review both frameworks and explain why they are relevant to the work conducted in this doctoral thesis.

1.4.1 Behavioural self-regulation accounts

Behavioural self-regulation accounts (Bachevalier & Loveland, 2006; Hellendoorn, 2014; Loveland, 2005; Loveland, 2001) propose that the observed social difficulties in ASD could stem from an impairment in the mechanisms underlying the processing of social cues and/or the regulation of behaviours in response to these social cues. In other words, they could not only be characterised by processing deficits but also by a failure to perceive and/or act upon the social functional meaning of these cues in a typical way (Gibson, 1979; Loveland, 2001; Zebrowitz-McArthur & Baron, 1983).

This ecological view of autism was put forward by Loveland (2001) and more recently Hellendoorn, (2014) who argue that autism reflects a “disordered relationship between the person and the environment” (Loveland, 2001, page 23). It has its basis on the concept of affordances proposed by Gibson, (1979), which was used to characterise visual perception and psychological explanations of behaviour in general. The term affordances is better understood as part of an organism-environment system where the environment provides or affords to the individual opportunities for action and perception according to the meaning of surrounding objects, persons and the current needs of the perceiver. For example the decision to lift a heavy object or not depends on the interaction of the properties of the object (how heavy it is, what dimensions) and the potential lifter’s characteristics (their size, their strength). Similarly, behavioural self-regulation accounts on emotion perception domains propose that socio-emotional signals work in a similar manner offering opportunities for action to the observer and allowing them to regulate their behaviour. An angry facial expression for instance would serve the purpose of signalling the rage of the expresser to the observer but most importantly it would trigger avoidance behaviour to the observer, who in this case would be likely to run away. Self-regulation depends on the ability to first perceive the emotional signal and infer relevant information, such as the meaning of the emotion and its significance to this observer (Loveland, 2005; Loveland, 2001). Such inferences by the observer inform him of the intentions of the interlocutor which are essential for the second part of the self-regulation process. This includes adapting ones’ behaviour according to this signal and is an essential adaptive process that appears from very early in life and allows individuals to regulate their behaviour in response to the social world (Cicchetti & Tucker, 1994).

Thus, emotional expressions can be thought as communicative signals which trigger behavioural adaptation and individuals with ASD would present deficits not only to process these signals but also regulate their behaviour in response to these signals. Evidence leading to this view comes from observation studies which investigate the reaction of individuals with ASD to other people’s emotional situations, such as distress, fear, discomfort and so on. Children with ASD were compared to TD and ID children in regard to their responses to distress, discomfort and fear expressed by their parents or by the experimenter while the children were playing with toys (Sigman, Kasari, Kwon, & Yirmiya, 1992). While the two non-ASD groups turned their attention to the distressed adult, children with ASD looked at the adult significantly less and continued to play with their toys when the adult pretended to be hurt. In a different study, while all participants attended to the hurt individual, children with ID showed heart-rate deceleration in response to an adult’s high levels of distress, but this was not the case in the ASD group, suggesting that this group was neither aroused by the distressed individual nor overtly intending to avoid them (Corona, Dissanayake, Arbelle, Wellington, & Sigman, 1998). Other studies have also shown reduced responses to others’ facial affect in ASD (Bacon, Fein, Morris, Waterhouse, &

Alien, 1998; Loveland & Tunali, 1991; Yirmiya, Sigman, Kasari, & Mundy, 1992), a behaviour which is stable and at pre-school can predict the responsiveness of the same group 5 years later (Dissanayake, Sigman, & Kasari, 1996). Importantly, the level of responsiveness is associated with the level of functioning of the individuals with ASD. Low functioning children with ASD showed striking deficits in responding to another's distress across different situations, with 45% not orienting their attention to the distressed individuals at all (Bacon et al., 1998). Lastly, in scenario where A is tearing apart a drawing of individual B children with ASD did not anticipate the B's distress although TD children and children with learning disabilities oriented towards them (Hobson, Harris, García-Pérez, & Hobson, 2009).

These findings might not directly assess behavioural adaptation in response to emotion signals but they provide the basis for understanding the reported reduction in responsiveness to another's affect in ASD. They suggest that this group does not learn to engage in avoidant behaviours in response to aversive stimuli and that they miss opportunities to learn about the meaning of another's affective state. According to this view, individuals with ASD could present deficits not only in the mechanisms behind the processing of emotional displays but also in the mechanisms responsible for the regulation of adaptive responses to these displays. It is implied that an impairment such as this at either of these two levels would give rise to the apparent lack of social interest observed in this group and would explain part of their socio-communicative deficits.

1.4.2 Social motivation accounts

On the other hand, social motivation accounts of autism (Chevallier, Kohls, et al., 2012; Dawson et al., 2005) stem directly from atypicalities in the 3 key aspects that constitute social motivation in neurotypical individuals. These include social orienting, social seeking or liking (reward) and social maintaining. In typical development individuals spontaneously orient their attention to relevant social cues in the environment, they find social interactions rewarding and thus they try to maintain them.

Deficits in social orienting are characteristic of ASD from a very young age (Elsabbagh et al., 2012) and they are among the first symptoms of the condition to have ever been reported (Kanner, 1943). People with ASD indicate reduced interest in the human face (Jemel et al., 2006), atypical attention allocation with non-social stimuli being preferred over social ones and preserved sensitivity to eye contact (Riby & Hancock, 2008; Senju & Johnson, 2009). Children with ASD tend to focus mostly on the background rather than the characters chatting in social scenarios (Riby & Hancock, 2008) and children and adolescents with ASD fixate less on social aspects of clips including faces and eyes (Klin et al., 2002). Moreover, while neurotypical individuals find social interactions highly rewarding, individuals with ASD show selective social anhedonia, reporting diminished pleasure in social interactions

(Chevallier, Grèzes, Molesworth, Berthoz, & Happé, 2012). In support of this, ASD is characterised by abnormalities in the orbitofrontal-striatum-amygdala circuit in response to social stimuli (Schultz et al., 2000) which could stem from atypical representation of the reward value of those stimuli (Dawson et al., 2005). This circuit plays a pivotal role in emotional decision making and the valuation of hedonic experiences (Bachevalier & Loveland, 2006; Schultz & Tremblay, 2010). Lastly, since neurotypical individuals find social interactions rewarding, they tend to engage in maintaining strategies to preserve these interactions, such as reputation management and flattery. However, individuals with ASD do not seem to engage in the same strategies. A recent study (Chevallier, Molesworth, & Happé, 2012) investigated reputation management in ASD by giving children a set of drawings, some of which were considered good, others bad and others neutral. They then asked participants to rate them. The presence of an experimenter stating that one of the drawings was theirs lead to inflated ratings of the quality of this drawing in TD children as compared to their previous ratings of the same drawing. The same was not the case in ASD who did not seem to be influenced by the presence of the person whose drawing it supposedly was and they did not engage in flattery. This was associated with their social anhedonia levels, which is an index of the pleasure children find in social situations. Taken together, differences between neurotypical and ASD individuals in those three domains suggest that social motivation could be deficient in autism and that individuals with ASD assign less weight to social information.

This view, in contrast with the self-regulation accounts, does not assume deficits in the mechanisms behind social abilities but rather implies that these are manifestations of a deficit in social motivation. In regard to the processing of facial affect and particularly to the processing of threatening emotions, which are primarily expressed in the upper face, deficits in social orientation are central for the study of ASD. In section 1.3.4, I explained how these individuals focus more on the mouth, they do not spontaneously orient to the eye-region of faces (Corden et al., 2008; Klin et al., 2002; Pelphrey et al., 2002; Spezio et al., 2007) and this constitutes one of the reasons for their failure in several social tasks. Social motivation accounts imply that under motivating conditions individuals with ASD should be able to perform similarly to controls and do not assume a failure in the mechanisms behind emotion processing or the regulation of appropriate response to this emotion. Such conditions could be achieved by explicit or implicit orientation of participants' attention to relevant social cues, for example through implementation of a fixation point in the eye-region of the stimulus. This is very important in the study of emotion processing and responsivity in ASD, where orientation to social cues is not spontaneous, because for adequate processing of social signals, the face of the emitter should be effectively attended to (Waters, Mogg, Bradley, & Pine, 2008).

A recent study tested a group of TD and a group of ASD children on a Stroop task with social or non-social distractors (Figure 11A from Chevallier et al., 2013). Participants completed the Stroop task with either social distractors which included closed and opened eyes or non-social distractors which included flowers. In each condition there were neutral trials, where there was no word describing the colour but just coloured strings of the letter X, and incongruent trials, where the colour name was written in a different colour than the one stated. When social and non-social distractors were compared the two groups behaved in different ways with the ASD group getting larger Stroop interference, defined as the difference in RTs between incongruent and neutral XXX trials (Conty, Gimmig, Belletier, George, & Huguet, 2010), in the non-social condition while the TD group showed greater Stroop interference in the social condition (Figure 11B from Chevallier et al., 2013). Within social stimuli however, when comparing open with closed eyes and in the absence of non-social distractors, TD and ASD children behaved similarly showing greater Stroop interference in the salient social condition, where eyes were open (Figure 11C from Chevallier et al., 2013) giving a sense of being

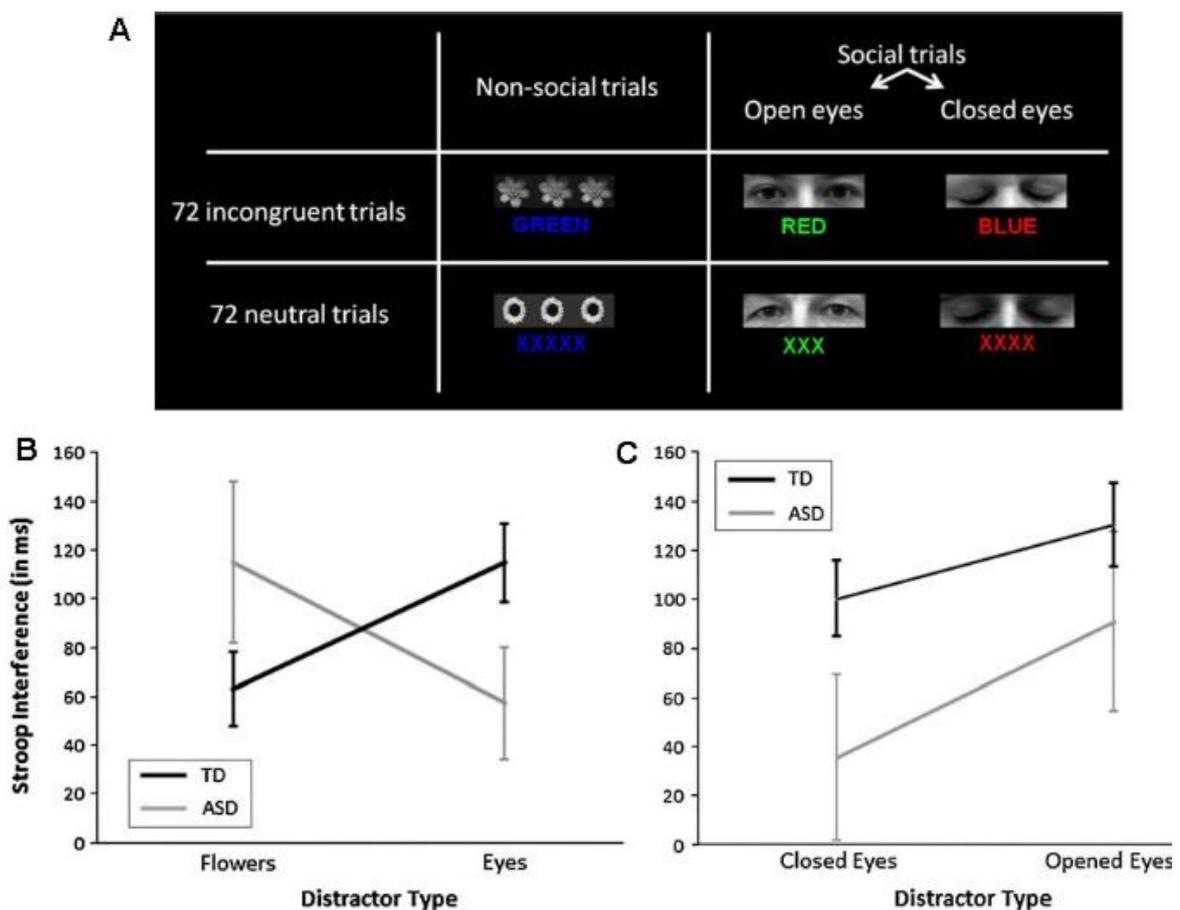


Figure 11 : from Chevallier et al., (2013). A) Stroop task in the presence of social and non-social distractors. B) Stroop interference per group when comparing non-social (flowers) and social (eyes) distractors. C) Stroop interference per group when comparing conditions within the social conditions (closed vs open eyes).

watched (Conty et al., 2010). Thus regardless of non-salient stimuli being prioritised in ASD, in their absence salient social stimuli are prioritised in a similar fashion as in typical development. This task proposes another useful way to study social abilities in ASD without disadvantaging participants with ASD and it involves experimental paradigms in the absence, or implicit presence, of non-social distractors.

To conclude, social motivation accounts predict the opposite of the behavioural self-regulation account. A lack of social interest would account for the social difficulties of this group to process and/or use social signals, while the underlying mechanisms for doing so are intact.

Chapter 1 conclusion

Whilst a large part of the literature is dominated by the idea of an overall emotion processing impairment in individuals with ASD, the above review suggests that under specific conditions, individuals with ASD are able to accurately decode expressed emotions and contradicts the idea of an overall impairment in processing facial affect. Behavioural self-regulation and social motivation accounts present two relevant alternatives for the explanation of emotion deficits in ASD. The former suggests that not only the mechanism behind emotion processing could be deficient in ASD but also the mechanisms behind the preparation of adaptive responses could be impaired too, because perceiving another's' expression would not be useful if the meaning of the expression is not understood. The social motivation theory presupposes that none of the mechanisms is impaired in ASD but rather diminished social motivation could account for the behavioural failures in social tasks and under motivated conditions such behavioural manifestations should be reduced.

The aim of this Ph.D. is to try and disentangle these two hypotheses by investigating the processing of and responding to social threats in adolescents with ASD. We used social threats, and more specifically facial expressions of anger and fear, because these emotions trigger direct behavioural adaptations in the observer (Darwin, 1872). In chapter 2 I will present a study on the processing of social threats in ASD, which will be investigated by looking at contextual effects of gaze direction, a social cues which in typicality enhance the saliency of threat (El Zein, Wyart, & Grèzes, 2015). In chapter 3 I will present a study on the regulation of adaptive responses to these two emotions in adolescents with ASD. Given the theoretical frameworks presented above three possibilities arise: individuals with ASD as compared to neurotypical controls will either 1) present deficits in the mechanisms behind the processing of and/or responding to social threats expressed in the face, 2) process social facial cues in the same way as neurotypical individuals and observed differences would result from a failure to grasp the communicative value of these facial cues, leading to failures to adapt their behaviour or 3) they will present intact behaviour during both the processing and use of social threats for behavioural adaptation.

Chapter 2: Processing of social threats in adolescents with autism spectrum disorders

In this chapter, I will present the theoretical framework relevant to the first experiment of my Ph.D., followed by the first completed experiment on the processing of threatening emotions in adolescent with ASD (Ioannou et al., 2017). Firstly, I will present the background literature for contextual influences on emotion processing in neurotypical populations, with a specific focus on the contextual influence of gaze direction on the decoding of threatening emotion. Secondly, I will describe existing studies investigating this integration in individuals with autism spectrum disorders. Lastly, I will present the first study of my Ph.D. that investigated the processing of threatening emotions, namely anger and fear, by looking at the impact of contextual gaze direction on the decoding of these emotions and the mechanisms underlying this influence in adolescents with and without ASD.

2.1 Contextual effects on emotion processing in neurotypical populations

The majority of the studies mentioned in the previous chapter focus on the recognition and decoding of facial expressions of emotions presented in isolation. However, in real life situations one's facial expression, like any visual object or feature, is always presented as part of a surrounding context which, in turn, influences the way the facial expression is perceived (Bar, 2004; Barrett, Lindquist, & Gendron, 2007). Context can be provided in several ways; by the surrounding environment, by the state of the observer and/or the state of the emitter. In terms of the surrounding environment, neurotypical adults are quicker at decoding an emotion when this is presented in an emotionally congruent background, such that a positive background facilitates the decoding of a positive emotion and a negative background of a negative one (Righart & de Gelder, 2008). In a study by Righart & de Gelder (2008), participants were quicker at recognising emotions within emotionally congruent environments, such as



Figure 12 : Example of an emotionally congruent (left) and an emotionally incongruent stimulus (right) from Righart & de Gelder, (2008).

a joyful face among flowers or a disgusted face among rubbish, as compared to the inverse (see Figure 7). In terms of observer related contextual influences, individual differences can also have an impact on the decoding of emotions, such that clinically and non-clinically anxious individuals are biased to interpret surrounding stimuli and events as more threatening than they are (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007). Lastly, contextual influences on emotion decoding can derive from the integration of concomitant socio-emotional cues produced by the emitter, which can be either *within-sender* or *within-face* features (Wieser & Brosch, 2012) and combined they can produce the perceived social signal (see Figure 13 from Vinciarelli, Pantic, & Bourlard, 2009). Examples of within-sender cues include body postures and gestures or changes in the head direction while examples of within-face features include changes in the dynamics of the face or in the direction of the gaze. When these additional non-verbal communicative cues are taken into account during perception of emotion, they have been shown to contribute to better identification of the emitter’s state, because of signifying the expresser’s focus of attention, whether the observer or not, and because they effect on the saliency of the emotion in neurotypical adults.

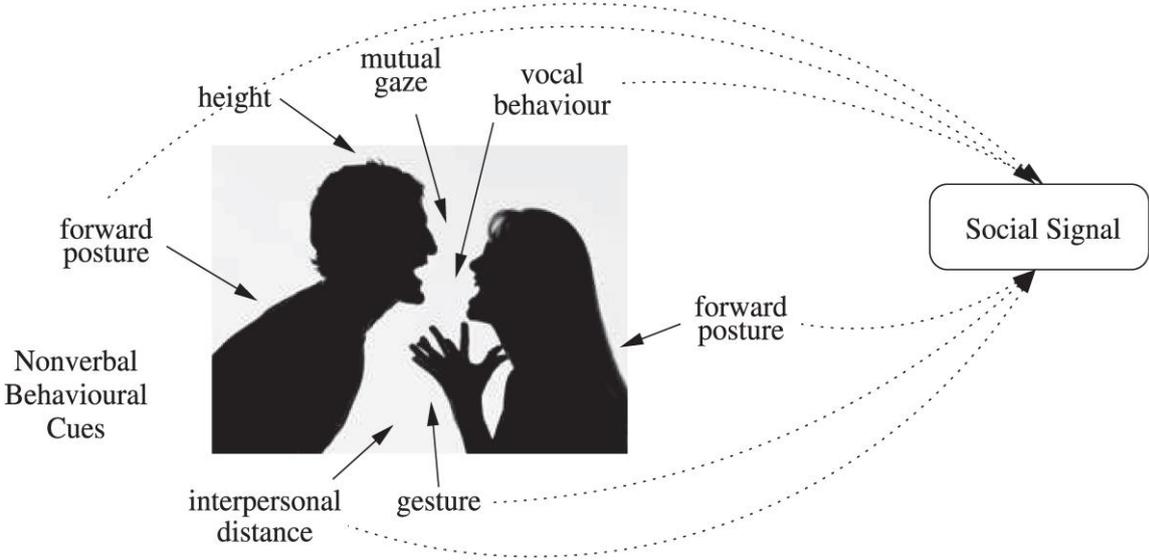


Figure 13: A social signal is produced by the integration of different concomitantly emitted cues, including facial expressions of emotion, gaze direction, hand movement and gestures (from Vinciarelli et al., 2009).

Hess, Adams, & Kleck, (2007) exposed participants to repetitions of angry, happy, fearful, sad and neutral facial expressions while they manipulated the direction of the expresser’s head. They found that this manipulation had an effect on the processing of emotions but this effect was particularly strong for the emotions of fear and anger. Subjects identified anger more accurately when it was expressed by a face directed to them because it signals a direct, imminent threat to the observer, while fear was more accurately decoded when the expresser’s head was averted because it could signal a potential threat in the surrounding environment. These combinations, and particularly direct head

anger, elicited the lowest levels of approach tendencies. Furthermore, congruency between body posture and facial expressions facilitates the categorisation of the expressed emotion, such that withdrawal bodies lead to better and quicker identification of the expressed emotion, while emotional incongruence between the two can hinder performance (Meeren, van Heijnsbergen, & de Gelder, 2005). Recently, Conty, Dezechache, Hugueville, & Grezes, (2012) investigated the neural timing of the integration of both within-sender and within-face signals during emotion processing. To do so they manipulated the expresser's facial expression which was either neutral or angry, their gaze direction and their pointing gesture (Figure 14). The gaze direction was either direct or averted and the pointing gesture was towards or away from the observer. Importantly, gaze and pointing directions were always congruent. The behavioural results showed that direct gaze and direct pointing enhanced the observer's feeling of self-involvement and increased the behavioural relevance of anger to the observer. Imaging results showed an early coupling of these three social cues in the premotor cortex (PM), which took place approximately at 210ms after stimulus onset, possibly, as the authors suggest for the preparation of an appropriate adaptive response. Within-sender signals are very important for emotion decoding and they seem to integrate early in the brain potentially for the preparation of adaptive responses in the observer.

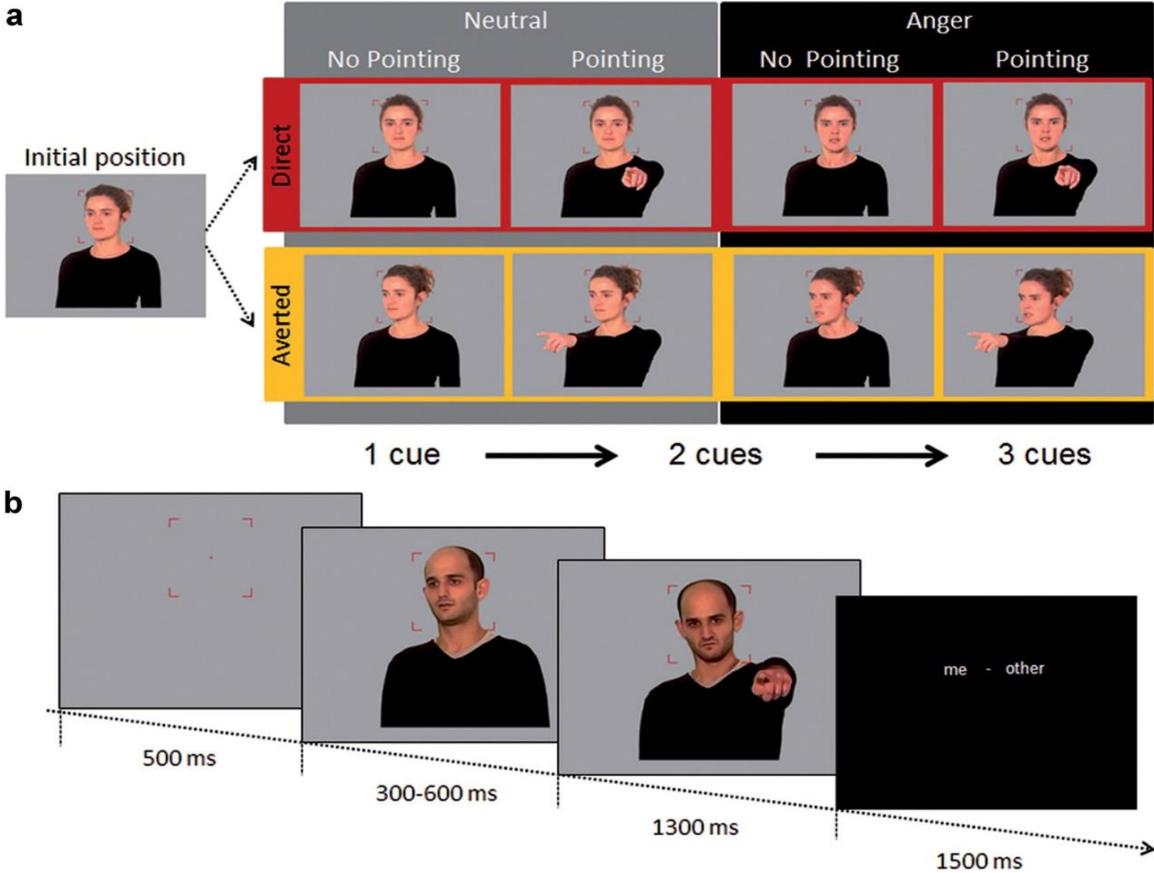


Figure 14 : a) Experimental conditions and b) trial example from Conty et al., (2012).

Similarly, within-face perceptual cues play a fundamental role in shaping social judgments and influencing social outcomes (Todorov, Olivola, Dotsch, & Mende-Siedlecki, 2015) as well as engage the PM for preparation of appropriate responses (El Zein et al., 2015). Gaze direction can act as contextual cue influencing the decoding of emotions. Specifically a series of studies have shown that in typical development contextual effects of gaze direction lead to better, more accurate and quicker identification of the expressed emotion (Adams et al., 2012; Adams & Kleck, 2003, 2005; Cristinzio, N'Diaye, Seeck, Vuilleumier, & Sander, 2010; El Zein et al., 2015; N'Diaye, Sander, & Vuilleumier, 2009; Sander et al., 2007; Sato, Yoshikawa, Kochiyama, & Matsumura, 2010). Specifically, neutral expressions are categorised as expressing anger or joy when they were coupled with direct gaze, while when the neutral faces were coupled with averted gaze participants categorised them as expressing fear or sadness (Adams & Kleck, 2005). Moreover, angry expressions are judged as more intense when they were presented with direct gaze as compared to averted, while fearful expressions are judged as more intense when they were coupled with averted than with direct gaze (see Figure 15 from Sander et al., 2007). These combinations are more arousing and elicit greater rapid facial reactions (RFR) than the inverse combinations (Soussignan et al., 2012). These findings suggest that the direction of the expression, signalled by the direction of gaze, increases the threat's salience and thus its behavioural relevance to the observer.

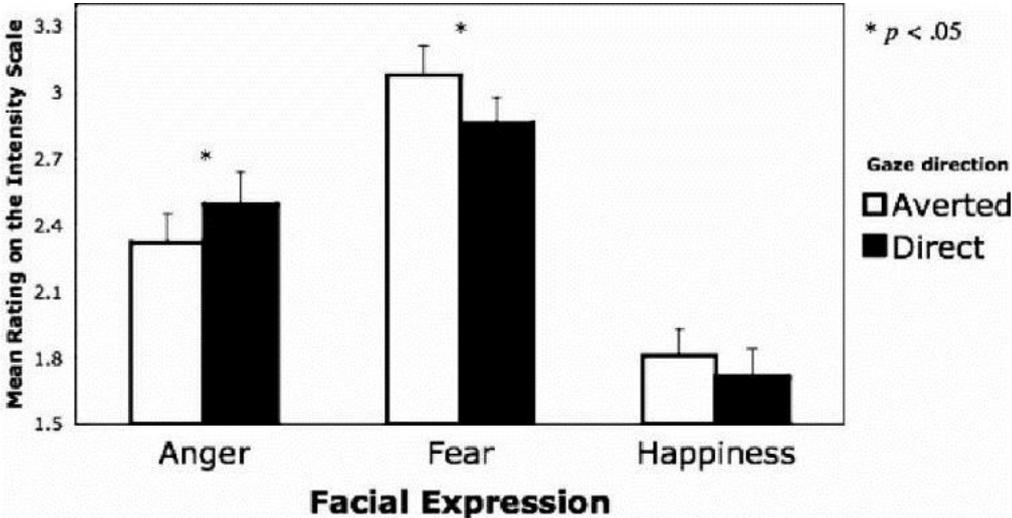


Figure 15: Intensity ratings of facial expressions of anger, fear and happiness when paired with direct and averted gaze (from Sander et al., 2007).

This is particularly relevant to anger and fear because they signal threat, mediating defence responses in the observer. Anger with direct gaze and fear with averted are considered more salient combinations of threat than the inverse. The former signifies that the observer is under direct, imminent threat, the latter could signal a potential threat in the surrounding environment. El Zein et al., (2015) using Signal Detection Theory (SDT; Green & Swets, 1966) disentangled between two

mechanisms that could underlie such an influence and found that gaze direction increases the observer's perceptual sensitivity to the emotion: in the case of anger for example when there is not much evidence for anger, which is provided by expression of reduced emotional intensity (e.g. closer to neutral - 0% anger) direct gaze would increase the sensitivity to the elements characteristic of anger. Similarly, when there would not be enough evidence for fear (low intensities of fear) averted gaze would enhance the sensitivity to perceptual characteristic of fear. Imaging results revealed a sustained enhancement of the perceptual sensitivity parameter specific to salient combinations of threat in face selective areas at 170ms following the appearance of the face. Importantly, only salient combinations resulted in an early (200ms following stimulus onset), significant neural encoding at motor preparation areas characteristic of fast responses. Given the co-evolved relationship between emitter and recipient and the communicative function of emotions for behavioural adaptation (Dezecache, Jacob, & Grèzes, 2015), such results suggest that gaze direction increases the sensitivity to, or salience of the emotion for motor preparation and selection of an adaptive response, such as approach or avoidance, in neurotypical individuals.

2.2 Contextual effects on emotion processing in autism spectrum disorders

What about contextual effects of gaze direction on emotion processing in ASD? To our knowledge only four studies have investigated the integration of these two socio-emotional signals in this group. Akechi et al., (2009) investigated this integration in children 9-14 years old with ASD as compared to a matched group of TD children. In the first experiment, faces expressing anger and fear were presented paired with direct or averted gaze. TD children indicated faster categorization of emotions in the salient combinations of threat, anger-direct and fear-averted gaze, compared to the opposite ones. However, the ASD group was not characterized by shorter the RTs in response to salient combinations of threat (see Figure 16 from Akechi et al., 2009). In a second experiment they replicated their findings using only the eye-region of the same stimuli in the emotion categorization task, because individuals with ASD are characterized by reduced spontaneous attention to relevant social stimuli, such as the eye-region of the interlocutor (Klin et al., 2002). However, these group difference were specific to the integration of cues and no differences were found in overall accuracy and RTs. The authors concluded that individuals with ASD cannot integrate the two cues because of a difficulty in extracting emotional information from the eye-region of the interlocutor. In a subsequent event-related potential (ERP) study Akechi et al., (2010) tested the same paradigm in ASD (10-17 yrs) and TD (9-16 yrs) children and adolescents. An integration of gaze direction and facial expression of emotion was revealed only in the TD group. These salient combinations of threat elicited larger N170 amplitudes in the TD group, an ERP component that reflects face processing. This was not the case in ASD children. This study reveals early (170 ms) integration of these socio-emotional signals in TD children and adolescents, which, the authors conclude, is impaired

in ASD. Similarly, in an functional magnetic resonance imaging (fMRI) study assessing the integration of facial expressions of fear with gaze direction in adults with and without ASD (Zürcher et al., 2013), the TD group showed greater activity in the ventral part of the anterior insula and anterior cingulate cortex in response to averted gaze, brain areas which are associated with the processing of socio-emotional information (Kurth, Zilles, Fox, Laird, & Eickhoff, 2010), appraisal and regulation of negative affect respectively (Etkin, Egner, & Kalisch, 2011). The same was not the case for the ASD group. Lastly, Tell, Davidson, & Camras, (2014) found no contextual influence of gaze direction in neither TD nor ASD adults. All above studies concluded that the ability to integrate gaze direction with threatening emotion in ASD is somewhat impaired. However, not only is the research limited but the findings are highly inconsistent. Critically, before reaching conclusions the methodological details of these studies and specific requirements for the targeted population need to be addressed (see Table 1 and refer to section 1.3).

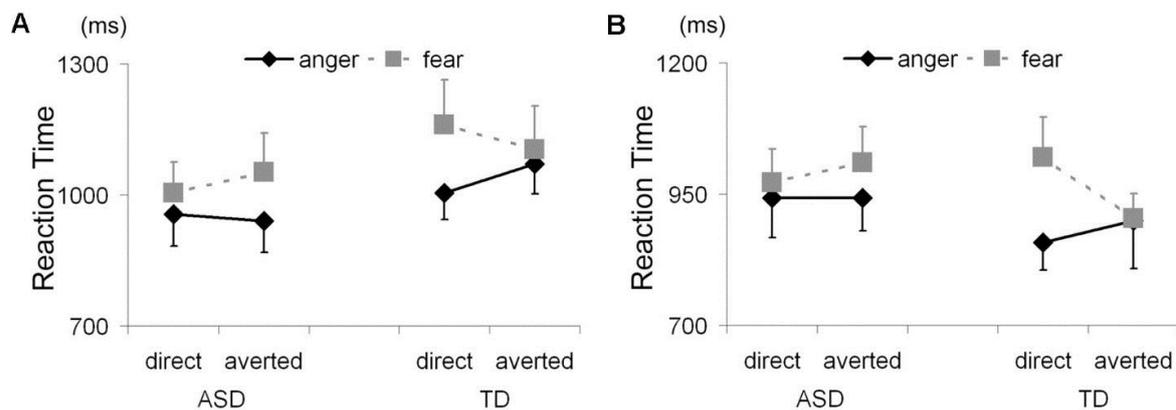


Figure 16: Emotion categorisation RTs for fear and anger coupled with direct and averted gaze in TD and ASD children (from Akechi et al., 2009) when using A) full face stimuli and B) only the eye-region of the stimuli.

In the absence of a study that takes into account those methodological limitations, a conclusion that individuals with ASD cannot integrate contextual gaze direction during threat processing seems premature especially given very recent evidence in adults with ASD pointing to typical integration of facial expressions of emotion and body postures (Brewer, Biotti, Bird, & Cook, 2017). Importantly in the 3 studies reviewed in table 1 that required a response, there were no overall emotion decoding accuracy or RT differences between groups, supporting the evidence in favour of intact emotion processing in ASD, which was reviewed in chapter 1, section 1.3. Lastly, these studies offer a new way of assessing inconsistencies in threat processing, or emotion processing in general, in ASD, allowing us to investigate not only detection and decoding of socio-emotional signals but also their integration.

Methodological details Experiment	Sample size (females)		Mean age in years		Matched?	Stimulus duration	Response window	Fixation (length)	Emotion strength	Accuracy/RT group differences
	ASD	TD	ASD	TD						
1) Akechi et al., (2009) exp.1	14 (4)	14 (4)	12.1	11.9	Age, gender, IQ, IQV, IQP	Until response (max 5000ms)	max 5000 ms	Nose (750 ms)	100%	No
2) Akechi et al., (2009) exp.2	10 (3)	10 (6)	12.4	11.3	Age, gender, IQ, IQV, IQP	Until response (max 5000ms)	max 5000 ms	Nose (750 ms)	100%	No
3) Akechi et al., (2010)	14 (4)	14 (6)	13.7	12.3	Age, gender, IQ, IQV, IQP	1200 ms	Until response	Eye-region (1000 ms)	100%	No
4) Zucker et al., (2013)	22 (3)	22 (3)	27.6	23.7	Age, gender, IQP	300 ms	No response required	Eye-region (1200ms)	100 %	NA
5) Tell et al., (2014)	22 (5)	22 (5)	10.3	9.8	Age, gender	Until response	Until response	No fixation	50 %, 100 %	Yes: fear and sadness

Table 1: Methodological details for all five studies that have investigated the integration of gaze direction and facial expression of threat in individuals with ASD. These include the sample size, the mean age of the participants in each group, the variables on which the two groups were matches, the stimulus duration and the response window, the implementation of a fixation point or not and its position on the subsequent stimulus, the intensity of emotions used and overall group differences in emotion accuracy or RTs.

2.3 Shared mechanism for emotion processing in adolescents with and without autism (Experiment 1)

In chapter 1 we saw that the literature for an overall deficit in the processing of facial displays of emotion in ASD is inconsistent and results seem to vary greatly depending on factors such as the paradigm of the study, the length of the stimulus presentation, the matching between groups and the implementation or not of socially motivated conditions. In chapter 2, section 2.1, we saw that the processing of emotion in neurotypical populations does not depend exclusively on the facial expression of this emotion but rather on its association with the context in which it is presented. Of interest here is the contextual effects of gaze direction on the perception of facial expressions of threat, namely anger and fear. Past studies have failed to show a contextual influence of gaze direction on the categorisation of threatening emotions in ASD. However, failure to do so in this group could stem from methodological inconsistencies across studies, for instance the use of exclusively stereotypical expressions of emotion - 100% intensity -, long presentation time of the stimulus and absence of a social attention jitter.

In the first study of this Ph.D. we are addressing the question of emotion processing in ASD by looking at the contextual influence of gaze direction on this processing while using a well-controlled paradigm that takes into account the methodological issues mentioned in section 2.2 (El Zein et al., 2015). We used stimuli, which were parametrically manipulated to represent 7 intensities of anger and fear, paired with direct and averted gaze. We chose a rapid stimulus presentation to tap into automatic, reflexive processing (Adams et al., 2012) and implemented an attention jitter to the stimulus eye region before its presentation to attract attention to the relevant social cues (Chevallier, Kohls, et al., 2012). We expected that, in the possible absence of an overall failure of the mechanisms behind emotion processing in ASD, under these conditions adolescents with ASD should be able to integrate gaze direction with facial expressions of threat. The second goal of this study, was to address the mechanisms behind the contextual influence of gaze direction on categorisation of threatening emotion, independently of differences in emotion recognition accuracy between the groups. In order to do so we performed Bayesian comparisons between decision-making models created using the framework of the SDT.

Signal Detection Theory (SDT)

In everyday life, when individuals are faced with decisions they do not passively receive sensory information to directly determine their decision, but they have to actively make perceptual judgments under uncertainty. The SDT (Green & Swets, 1966) is a framework that enables characterisation and understanding of decisions made in situations where sensory information is ambiguous, in other words in situation where there is noise. Put simply, imagine someone who walks down a busy town road on a

sunny summer morning looking for his car. This person will probably not perceive the sound of leaves thrusting on the trees because in this case it is just background noise. Now, imagine the same person at the same place but later at night, when there is no traffic and no noise. This time not only will the person hear the thrusting leaves in the background, but based on their ability to extract sensory information or in other words their sensitivity to sensory information, their detection will be modulated. According to the theory, detection of a signal depends not only on the intensity of this signal but also on the state or sensitivity of the observer to the signal.

The theory has its roots in engineering and it was firstly used in detection tasks. The simplest Yes-No design detection task (Tanner & Swets, 1954) resembles a lot the above situation. It involves a series of trials where a signal is either presented in isolation or in noise and the observer has to indicate the presence or not of the signal. This leads to four possible outcomes as seen in Figure 17A (from Macmillan, 2002) given the combination of the two possible responses (yes or no) and the two stimuli (noise or signal). In the second panel (Figure 17B) we can see the representation of the two Gaussian distributions, one for the noise and the other for the signal trials. The *decision criterion* c is the tendency or bias of the perceiver to respond that a signal is present. Decisions are assumed to be taken when the value of a noisy decision exceeds the

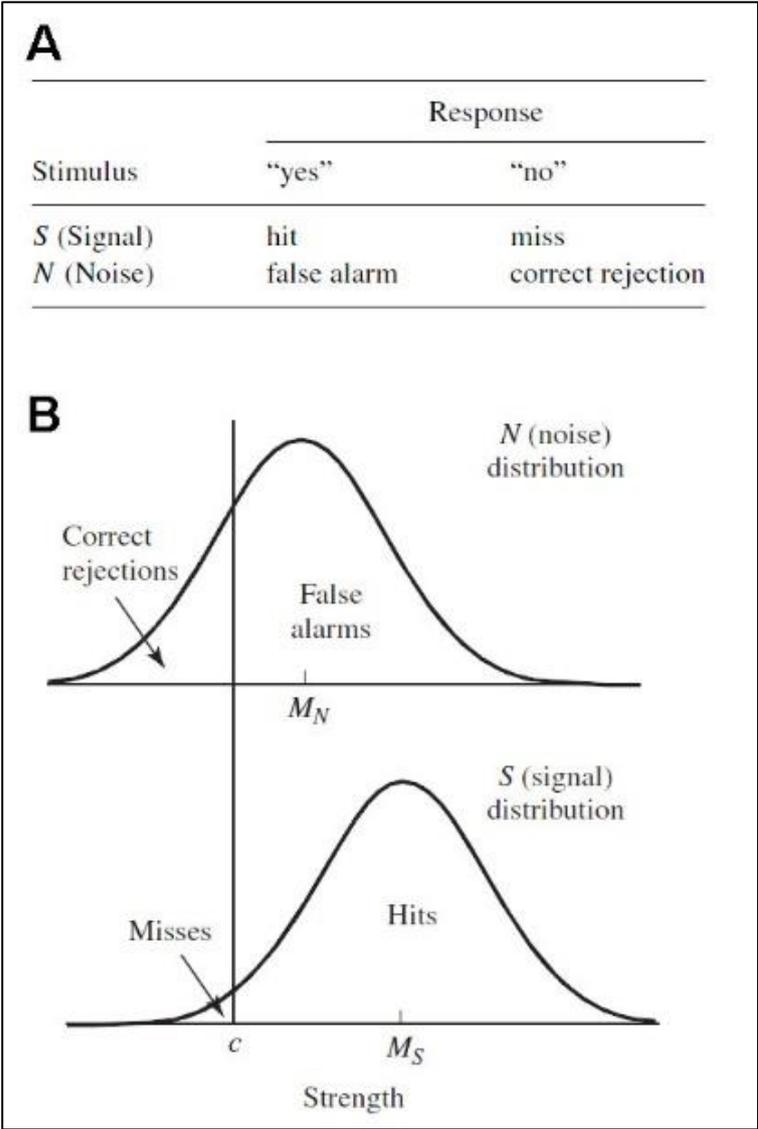


Figure 17: From Macmillan, (2002): A) Possible outcomes in a Yes-No design trial. B) The upper curve shows the Gaussian distribution of noise trials and the lower curve the distribution of signal trials. The parameter c refers to the decision criterion, M_N and M_S refer to the means of the distributions. Note that the variances are assumed to be equal.

decision criterion c . In the noise curve, values above the criterion c lead to false alarms while values below c lead to correct rejections. In the signal curve values above the criterion c lead to hits and values below it result in misses. When the two distributions overlap, creating situations of uncertainty, it is expected that errors will be made. The biggest advantage of SDT in psychology research is that it enables us to distinguish between the sensitivity parameter d' and a response bias, the decision criterion c . The sensitivity parameter d' refers to the signal-to-noise ratio, it describes how sensitive is the perceiver in distinguishing the signals from noise and depends on the overlap between the two distributions. The smaller the overlap between the two curves, the larger the sensitivity d' and the better the ability of the person to discriminate the signal from the noise. As mentioned above, the decision criterion c represents the individual biases of the decision maker and can be set at any point on the decision axis.

Similarly to the two choice Yes-No detection paradigms, the framework can be applied to two-alternative forced choice (2AFC) paradigms in the visual domain. For instance, in a motion discrimination paradigm participants see a large number of dots that move randomly across space introducing a random dot kinetogram with a percentage of coherent motion across the dots. Usually participants have to decide in which direction the dots move, for instance up or down. Let's imagine that the dots are moving upwards, which would be option 1 (signal), rather than down or option 2 (noise). According to SDT, participants' behaviour, under this uncertainty could be described by the following psychometric function:

$$p(\text{option 1}) = \Phi(w * x + b)$$

where the probability of choosing option 1 over option 2 (p) is given by the cumulative normal function Φ , where w is the sensitivity parameter, multiplicative by the sensory evidence x and b is an additive parameter which represents the individual's tendency to choose option 1 over option 2, for instance up over down, or signal over noise. In terms of the original detection task the multiplicative parameter corresponds to the sensitivity parameter d' and the response bias b corresponds to the response criterion c .

How will we use SDT to characterise mechanism behind the contextual effects of gaze direction on the processing of social threats in ASD? According to SDT and its capacity to distinguish between a response bias and a sensitivity parameter, there are two ways in which gaze direction could influence the processing of the emotions and this involves influencing either of these two parameters. Gaze direction could either bias the participants response at the selection level or it would affect the participants' perceptual sensitivity to the emotion at the processing level (for details see Figure 18 from El Zein et al., 2015 and section 2.1).

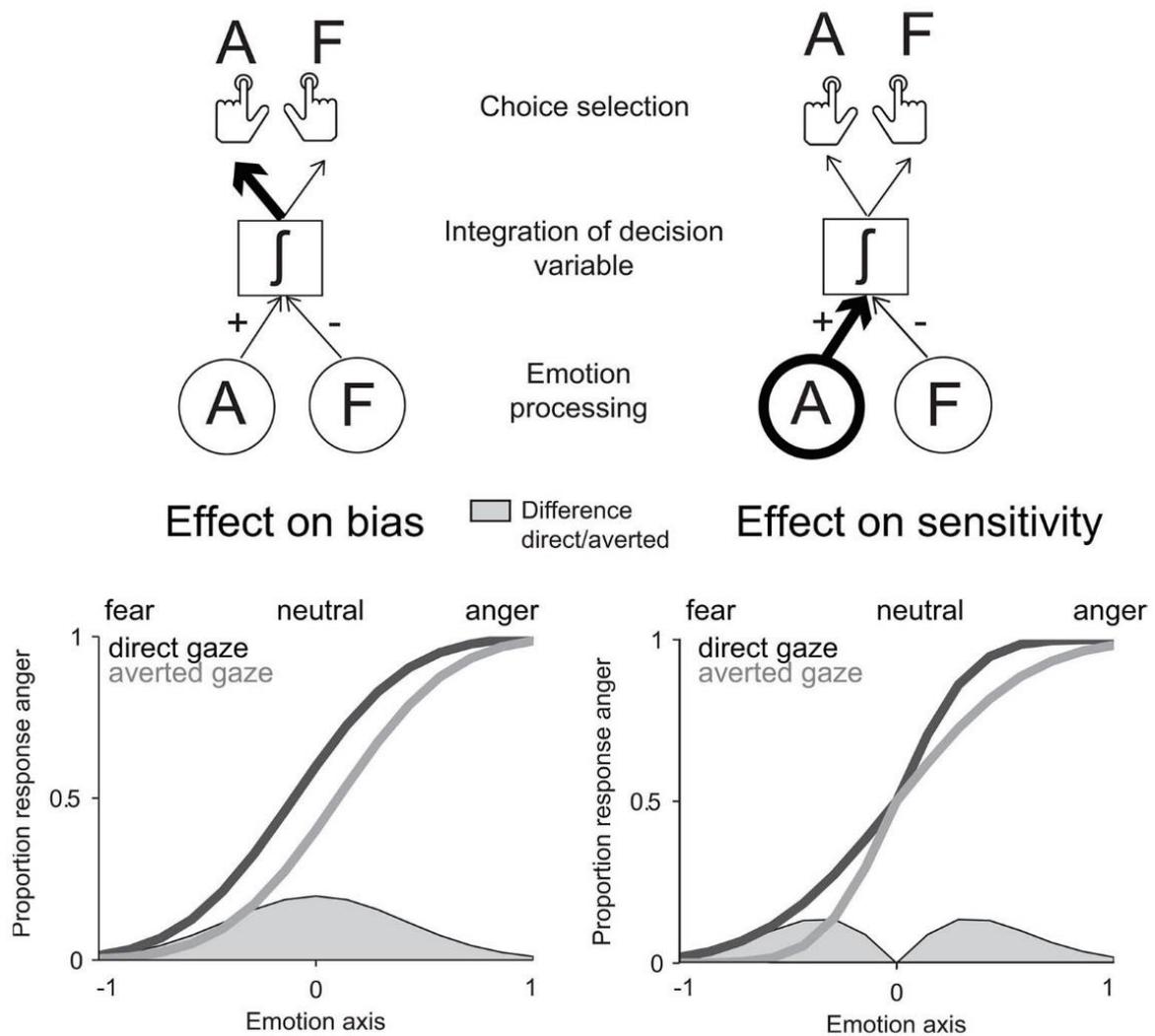
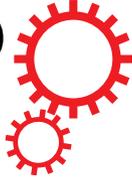


Figure 18: Model predictions for the contextual effect of gaze direction on emotion categorisation from El Zein et al., (2015). Left panel: description of the impact of gaze direction on the participants' choice selection. Gaze would additively bias the selection of anger (upper left panel) and the psychometric function would be shifted towards the left in direct gaze conditions, leading to the interpretation of faces with direct gaze as angry. This effect would be most evident in cases of high ambiguity, when the intensity of the emotional expression would be relatively low and maximal for neutral (emotionless) faces, as indicated by the frilled grey area across the emotion axis (lower left panel). Right panel: description of the impact of gaze direction on the participants' perceptual sensitivity, at the processing level. Gaze direction would increase the participants' sensitivity to the facial features characteristic of the emotion signalling higher threat with direct gaze enhancing multiplicatively the processing of angry facial expressions when paired with direct gaze (upper right panel). This would cause an increase in the slope of the psychometric function for salient combinations of threat and maximal effects would again be observed in cases of highest uncertainty, at low emotion strengths (lower right panel).

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Shared mechanism for emotions processing in adolescents with and without autism.

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Shared mechanism for emotion processing in adolescents with and without autism

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Although, the quest to understand emotional processing in individuals with Autism Spectrum Disorders (ASD) has led to an impressive number of studies, the picture that emerges from this research remains inconsistent. Some studies find that Typically Developing (TD) individuals outperform those with ASD in emotion recognition tasks, others find no such difference. In this paper, we move beyond focusing on potential group differences in behaviour to answer what we believe is a more pressing question: do individuals with ASD use the same *mechanisms* to process emotional cues? To this end, we rely on model-based analyses of participants' accuracy during an emotion categorisation task in which displays of anger and fear are paired with direct vs. averted gaze. Behavioural data of 20 ASD and 20 TD adolescents revealed that the ASD group displayed lower overall performance. Yet, gaze direction had a similar impact on emotion categorisation in both groups, *i.e.* improved accuracy for salient combinations (anger-direct, fear-averted). Critically, computational modelling of participants' behaviour reveals that the same mechanism, *i.e.* increased perceptual sensitivity, underlies the contextual impact of gaze in both groups. We discuss the specific experimental conditions that may favour emotion processing and the automatic integration of contextual information in ASD.

Autism spectrum disorders (ASD) are neurodevelopmental conditions characterised by significant deficits in social interaction and communication skills, associated with repetitive and restricted interests¹. Atypicalities in the affective domain are central to ASD and research suggests that individuals with ASD react to social cues differently from typically developing (TD) individuals^{2–4}. The roots of such difficulties are still debated but it has been suggested that difficulties in processing emotional cues^{3–5} play an important role in these social deficits. This hypothesis has led to a considerable amount of work that is partly synthesised in a meta-analysis of 48 studies involving nearly one thousand participants with ASD³. Overall, research points to emotion recognition difficulties and to reduced activation of emotion related brain areas in autism^{6,7}. However, a number of studies (including ones with large sample sizes and well-matched groups) have found that people with ASD do recognise emotions accurately^{8–10}. In this paper, we shift the focus to ask whether the *mechanisms* behind the processing of threat-related emotional expressions (anger/fear) are the same in ASD, irrespective of potential differences in accuracy between ASD and TD groups. To do so, we focus on the contextual impact of gaze direction on emotion recognition because it is theoretically possible to distinguish different mechanisms that may affect the integration of these social cues¹¹.

Emotional displays are often ambiguous and the context in which they are presented also informs emotional decoding. For instance, recognition of threat-related emotional expressions is often informed by gaze direction, especially in cases where the expression is ambiguous^{12–17}: TD individuals are more likely to judge a neutral face as angry when presented with a direct gaze and as fearful when presented with an averted gaze¹⁴. TD individuals are also quicker and more accurate to recognise anger presented with a direct gaze because it signals to the observer that they are under imminent threat, and fear with an averted gaze because it signals a potential threat in their surroundings¹⁶. These combinations of gaze direction and emotional expressions are thus more salient to the

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observer¹¹ compared to the reverse combinations (anger with averted and fear with direct gaze). Up until recently, the mechanisms through which these phenomena occurred remained unknown. Indeed, classical decision theory distinguishes two manners in which gaze direction might influence emotion categorisation: through a change in decision bias toward highly salient threat-signalling combinations or through enhanced perceptual sensitivity to these combinations. Recent work¹¹ suggests that improved decoding of specific combinations of gaze and emotion is associated with a selective enhancement of perceptual sensitivity in TD adults.

In ASD, it is unclear whether the impact of gaze direction on emotion categorisation is intact and whether the mechanisms they rely on are the same as those used by neurotypicals. Existing data suggest that highly salient threat combinations (anger-direct, fear-averted) are not recognized more quickly than less salient combinations in ASD and that they fail to elicit larger face-sensitive event related potentials (ERP) in ASD children^{18,19}. Similar results were also found in ASD adults, using fMRI²⁰. Taken together, these findings suggest that individuals with ASD may use different mechanisms to combine contextual information, specifically gaze direction, with emotional expressions of anger and fear when categorising emotions. However, a number of issues limit the scope and generalizability of these findings. Specifically, in these studies, the emotional expressions used were stereotypical, of high intensity, and of long duration. Yet, the automatic impact of gaze direction on emotion perception takes place in the brain within 200 ms after stimulus onset, for short stimuli presentation (<300 ms) and, is more prominent when the expression is ambiguous and hence more difficult to discriminate^{11,21,22}. Further, with the exception of one study²⁰, participants were not explicitly instructed to fixate the eye-region of the face despite evidence linking attention directed to the eye-region and emotion recognition performance²³. Since ASD individuals do not spontaneously orient to the eye region^{24–26}, the lack of explicit instruction may have put the ASD group at a disadvantage^{26–28}.

Given the issues reported above, the goal of the present experiment was twofold. First, we aimed to determine whether participants with ASD use gaze signals to inform emotional decoding of anger and fear under well-controlled experimental conditions. To do so, we adapted an emotion categorisation task¹¹ controlling for a range of potential confounds: emotion intensity was manipulated parametrically across seven levels of “morphed” facial expressions ranging from neutral to intense anger or fear; contextual information was included by pairing facial expressions with direct or averted gaze; participants’ attention was drawn to the eyes of the upcoming face by presenting a fixation cross right before the appearance of the stimulus; finally, faces were flashed for 250 ms in order to tap into the automatic (reflexive rather than reflective) stage of processing²². Our second goal was to determine whether, under such experimental conditions, the mechanisms behind threat-related emotion-gaze integration are similar in TD and ASD individuals.

Results

The experimental task was a two-choice emotion categorisation task (fear or anger). In each trial participants were presented with a facial expression of anger or fear of varying intensity (7 levels of emotion strength), paired with direct or averted gaze, and had to categorise the expressed emotion (see Fig. 1). The concomitant gaze direction was not mentioned to the participants and hence was implicit.

Participants completed 3 blocks of 120 trials. We first ran an ANOVA including blocks as a factor to investigate potential effects and interaction with blocks. An effect of blocks ($F(2,37) = 3.795$, $p = 0.032$, $\eta_p^2 = 0.170$) revealed that participants’ emotion accuracy increased over time with significantly better performance in the third block (85%) as compared to the first (80%). No other effects or interactions were significant, so block was not included as a factor in the remaining analysis. Overall, both groups performed above chance (ASD Median = 82%, $Z = 3.920$, $p < 0.001$, $r = 0.62$; TD Median = 88%, $Z = 3.920$, $p < 0.001$, $r = 0.62$) although adolescents with ASD reached a significantly lower mean accuracy level (82%) than TD adolescents (86%) (Effect of group: $F(1,38) = 4.479$, $p = 0.041$, $\eta_p^2 = 0.105$).

Increased accuracy with emotion strength in both TD and ASD adolescents. Categorisation performance of both groups increased with emotion intensity ($F(6,228) = 53.745$, $p < 0.001$, $\eta_p^2 = 0.706$). An emotion by intensity interaction ($F(6,228) = 12.433$, $p < 0.001$, $\eta_p^2 = 0.247$) led to enhanced categorisation performance with emotion strength for both anger (Effect of intensity on anger: $F(6,228) = 54.952$, $p < 0.001$, $\eta_p^2 = 0.591$) and fear (Effect of intensity on fear: $F(6,228) = 13.267$, $p < 0.001$, $\eta_p^2 = 0.295$).

Overall emotion and gaze direction effects. Both groups showed enhanced recognition of fear (ASD: 86%; TD: 89%) in comparison to anger (ASD: 78%; TD: 84%) (Effect of emotion; $F(1,38) = 10.625$, $p = 0.002$, $\eta_p^2 = 0.222$; no emotion by group interaction: $F(1,38) = 0.424$, $p = 0.519$, $\eta_p^2 = 0.011$). One possible explanation for this fear advantage is related to an enhanced saliency of fear signals, which are perceived as instinctive reactions to an overall threatening environment²⁹. This is suggested by a recent paper²⁹ in which the authors compared search efficiency for angry and fearful expressions, both being negative emotions signaling danger, embedded in a crowd of neutral faces. Contrary to the anger-superiority hypothesis, they found better performance for fearful faces, as in the present study. The authors proposed that while anger signals a direct-threat (and therefore an unambiguous source of threat), fearful faces signal an indirect and more diffuse threat, and are therefore more salient.

The only difference in performance between the two groups was that the TD adolescents performed better overall in direct gaze conditions ($Z = 3.659$, $p < 0.001$, $r = 0.58$) compared to averted gaze conditions, while emotion accuracy in the ASD group did not differ between the two ($Z = 1.493$, $p = 0.135$, $r = 0.24$; Gaze * Group interaction: $F(1,38) = 5.263$, $p = 0.027$, $\eta_p^2 = 0.122$). This is consistent with previous research demonstrating an overall advantage of TD individuals in direct gaze conditions^{30–32}.

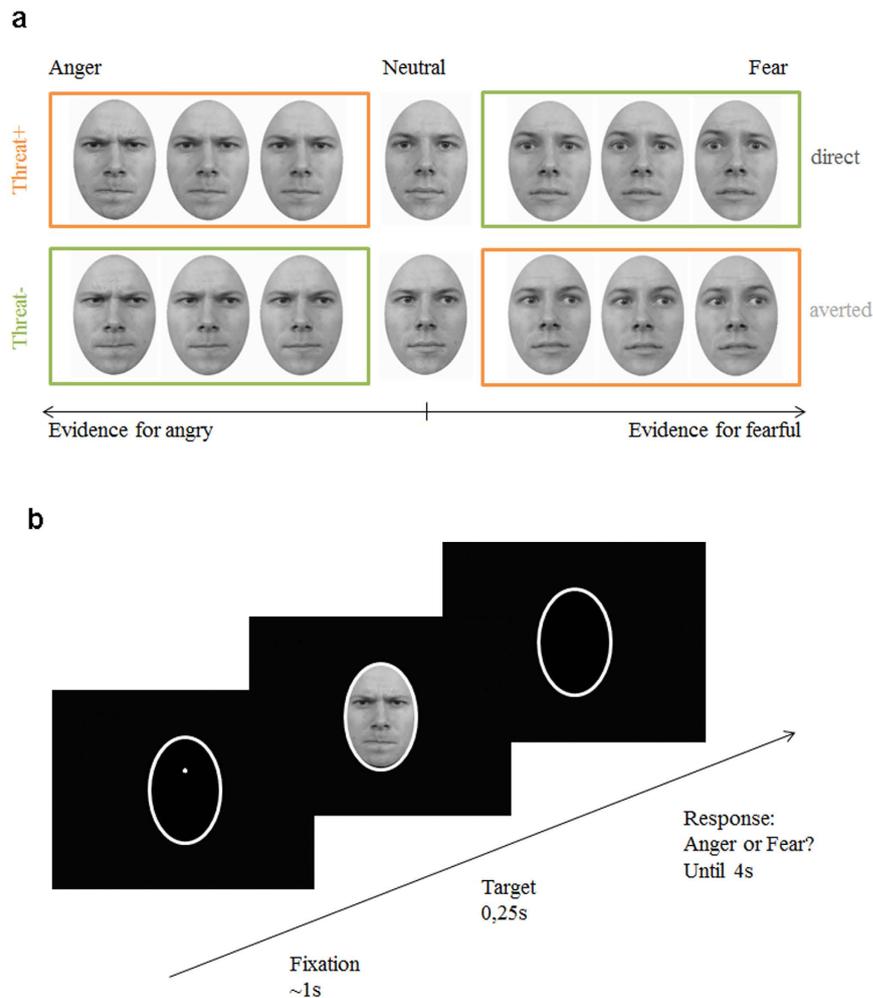


Figure 1. Stimuli and experimental procedure. (a) Example of facial expressions morphed parametrically from neutral to intense fearful/angry expressions providing evidence for one or the other emotion. Each face was either paired with a direct or an averted gaze. Threat+ conditions (in orange) correspond to combinations of gaze and emotion that signal higher salience and threat for the observer as compared to Threat– conditions (in green). (b) For each trial, and following a fixation (1 sec), a face appeared for 250 ms, and participants had a 4 second response window to indicate whether the face expressed fear or anger.

Increased recognition of threatening conditions in both TD and ASD adolescents. Contrary to previous studies in ASD^{18,19}, this study replicates in TD and ASD adolescents previous findings¹¹ in adults of an influence of contextual gaze direction on categorisation of threatening emotions (Emotion * Gaze: $F(1,38) = 26.242$, $p < 0.001$, $\eta_p^2 = 0.408$). We observed higher accuracy in the recognition of angry facial expressions when associated with a direct gaze as compared to an averted gaze, and higher accuracy in the recognition of fearful faces when associated with an averted gaze as compared to a direct gaze. Importantly, the present experiment reveals that this interaction did not differ between groups (Emotion * Gaze * Group: $F(1,38) = 0.287$, $p = 0.595$, $\eta_p^2 = 0.007$). Indeed, within group analyses revealed that the Emotion by Gaze interaction was significant in both the TD ($F(1,19) = 16.373$, $p = 0.001$, $\eta_p^2 = 0.463$) and the ASD group ($F(1,19) = 10.291$, $p = 0.005$, $\eta_p^2 = 0.351$) with both groups identifying highly salient threat combinations (anger-direct, fear-averted, labelled Threat+) better than less salient combinations (anger-averted, fear-direct, labelled Threat–; TD: $Z = 2.931$, $p = 0.003$, $r = 0.46$; ASD: $Z = 2.696$, $p = 0.007$, $r = 0.42$; see Fig. 2). Moreover, the variance of accuracy scores in Threat+ and Threat– were homogenous across the two groups (Threat+: $F(1,38) = 2.313$, $p = 0.137$; Threat–: $F(1,38) = 0.537$, $p = 0.468$).

Additionally, we computed the Bayes factor to test for the strength of the difference between Threat+ and Threat– in ASD as compared to TD³³ (see method section). We obtained a Bayes factor higher than 3 (Bayes factor = 32) when comparing the difference between Threat+ and Threat– in TD and ASD, confirming an increase in accuracy for Threat+ conditions in ASD group, similarly to the TD group.

Mechanisms underlying increased recognition of threatening conditions. To assess whether we replicate the increased perceptual sensitivity to threatening emotions found in healthy adults¹¹, we compared different models that could explain the participants' behaviour. In the framework of Signal Detection Theory³⁴,

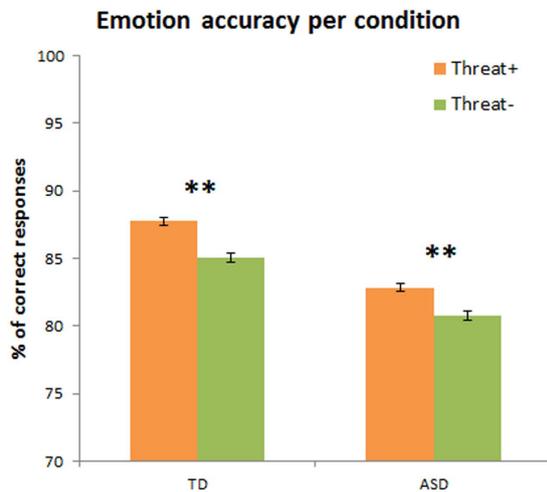


Figure 2. Emotion accuracy results for Threat+ and Threat– conditions for the TD group and the ASD group. Threat+ combinations were recognised more accurately than Threat– ones in both groups. Note that there was a main effect of group with the TD group demonstrating overall higher emotion recognition accuracy than the ASD group, but no interaction between group and Threat conditions. Within subject error bars represent Mean \pm S.E.; * $p < 0.05$, ** $p < 0.01$.

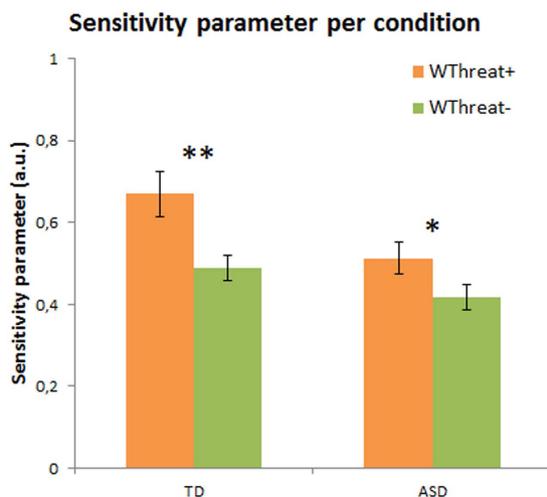


Figure 3. Perceptual sensitivity parameter estimate for Threat+ and Threat– combinations for the TD group and the ASD group. Both groups showed enhanced perceptual sensitivity for highly salient emotion-gaze combinations (Threat+). Error bars represent Mean \pm S.E.M.; * $p < 0.05$, ** $p < 0.01$.

an increased performance for Threat+ conditions could either stem from a *decision bias* toward these conditions (model 1), or from an increase in the *perceptual sensitivity* to these combinations (model 2) (see methods for details on the models and model comparisons). Fixed-effect Bayesian model selection (Bayesian information criterion) showed that an increased sensitivity to Threat+ conditions explained the data better than a change in the decision bias, in both TD and ASD groups (TD: Bayes Factor ≈ 93 , ASD: Bayes Factor ≈ 80). The sensitivity parameter estimate was significantly enhanced for Threat+ conditions as compared to Threat– in both the TD (Fig. 3; $p < 0.01$, standardized effect size = 2.7, see Methods for details) and the ASD (Fig. 3; $p = 0.03$, standardized effect size = 1.7, see Method for details) group (see Fig. 3).

Reaction time analyses. Although TD adolescents ($M = 350.8$, S.E.M. = 5.86) had faster general RTs (assessed by the Go/no-Go task) in comparison to the ASD group ($M = 380.4$, S.E.M. = 9.98; $U = 115.000$, $ASD = TD = 20$, $p = 0.021$, $r = 0.36$), to our surprise, ASD participants were quicker at responding during the emotion categorisation task as compared to the TD group (Effect of group: $F(1,38) = 13.819$, $p < 0.001$, $\eta_p^2 = 0.267$). Previous findings on RTs in ASD are mixed: some studies find that these individuals take longer than TD individuals to complete emotion categorisation tasks³⁵, others find no difference between the two groups^{18,36}, while still others, using several different visual search or detection tasks^{37,38}, report the opposite, finding ASD individuals quicker than TD individuals. Yet, it has been generally suggested that in individuals with ASD, better

visual search is associated with shorter RTs³⁸. Still, given that ASD showed faster general RTs associated with a decreased general performance, a speed-accuracy trade-off effect may be happening. We however believe that our main result, i.e. increased performance for Threat+ as compared to Threat- (interaction between gaze and emotion) cannot be explained by such potential speed-accuracy trade-off, as there was no significant interaction between gaze and emotion on RTs ($F(1,38) = 0.595$, $p = 0.445$, $\eta_p^2 = 0.015$; TD $F(1,19) = 0.192$, $p = 0.666$, $\eta_p^2 = 0.01$; ASD $F(1,19) = 3.914$, $p = 0.063$, $\eta_p^2 = 0.171$). Furthermore, we checked whether there was a correlation between general performance and RTs in ASD as a speed-accuracy trade-off proxy: a regression analysis revealed that mean RTs is not a significant predictor of ASD participants' mean performance ($F(1,19) = 1.070$, $p = 0.315$).

Gaze direction effects. We conducted RTs analyses to examine whether gaze direction has an influence on the speed with which participants decode the two emotions. Firstly, both TD and ASD adolescents' became quicker in responding when the expressed emotions were more intense, as reflected by the intensity by group interaction ($F(6,228) = 5.364$, $p < 0.001$, $\eta_p^2 = 0.124$; $F(6,114) = 6.286$, $p = 0.002$, $\eta_p^2 = 0.729$; ASD $F(6,114) = 6.558$, $p = 0.002$, $\eta_p^2 = 0.338$).

Secondly, in both groups, emotions presented with direct gaze were identified quicker than emotions coupled with averted gaze ($F(1,38) = 7.317$, $p = 0.01$, $\eta_p^2 = 0.161$). This could be linked to several previous findings: 1) direct as compared to averted gaze is generally easier to detect³⁹; 2) direct gaze leads to quicker RTs regardless of it being presented as part of a face or in isolation⁴⁰ and; 3) both ASD and TD individuals detect quicker targets with direct gaze than targets with averted gaze⁴¹.

Moreover, there was a Gaze * Group interaction ($F(1,38) = 4.171$, $p = 0.048$, $\eta_p^2 = 0.099$): ASD participants' RTs were comparable between direct and averted gaze ($Z = 0.747$, $p = 0.455$, $r = 0.12$) while the TD participants' RTs were quicker for direct gaze conditions as compared to averted gaze conditions ($Z = 2.501$, $p = 0.012$, $r = 0.39$), a result further confirming the better overall performance of TD individuals when the gaze is directed towards them in the present study.

Controlling for baseline RTs difference between group. Finally, in an attempt to control for potential baseline reaction time differences, we also ran our analyses while co-varying Go/no-Go RTs out. We found the same pattern of results: an effect of group ($F(1,37) = 17.986$, $p < 0.001$, $\eta_p^2 = 0.327$), no interaction between gaze and emotion ($F(1,37) = 1.567$, $p = 0.219$, $\eta_p^2 = 0.041$; TD $F(1,18) = 0.273$, $p = 0.608$, $\eta_p^2 = 0.015$; ASD $F(1,18) = 1.502$, $p = 0.165$, $\eta_p^2 = 0.104$). There was an intensity * group interaction ($F(6,222) = 5.066$, $p = 0.003$, $\eta_p^2 = 0.120$; TD $F(6,114) = 23.347$, $p < 0.001$, $\eta_p^2 = 0.551$; ASD $F(6,114) = 10.081$, $p < 0.001$, $\eta_p^2 = 0.347$), an effect of gaze ($F(1,37) = 5.779$, $p = 0.021$, $\eta_p^2 = 0.135$), with emotions with direct gaze better identified and this as a function of participants' general reaction times (Gaze * RTs general interaction, $F(1,37) = 7.293$, $p = 0.010$, $\eta_p^2 = 0.165$) and finally, a gaze * group interaction ($F(1,37) = 9.426$, $p = 0.004$, $\eta_p^2 = 0.203$).

To conclude, following the absence of a significant interaction between emotion and gaze direction on RTs in both groups, our results did not replicate the speed advantage for categorising Threat+ as compared to Threat- conditions previously demonstrated in TD adolescents¹⁸ and neurotypical adults¹¹.

Discussion

The present experiment aimed to determine whether the mechanisms behind emotion-gaze integration are similar in TD and ASD individuals, irrespective of potential group differences in accuracy. The results show that adolescents with ASD, similarly to TD controls, are more accurate when decoding highly salient combinations of gaze and emotion, demonstrating that they combine task-unrelated gaze information with emotion. Importantly, although TD participants had higher overall recognition accuracy than ASD participants, the fitting of decision theoretical models to the behavioural data revealed that, in both TD and ASD adolescents, gaze direction enhanced perceptual sensitivity to highly salient combinations, resulting in the associated improved accuracy.

These results stand in sharp contrast with previous observations^{18–20} showing that contextual gaze direction has little impact on emotion categorisation in ASD. However, our experimental set-up differs in several important ways. First, the ambiguity of sensory evidence was manipulated using graduated morphs moving from neutral to angry or fearful expressions. This is important because the impact of gaze direction is particularly clear in ambiguous situations where emotion discriminability is difficult^{11,42}. Second, the contextual cue (gaze direction) co-occurred with the decision-relevant stimulus but was irrelevant to the emotion categorization task, and thus did not need to be processed explicitly. Third, the facial expressions were presented for a very limited period of time, which allowed us to specifically tap into automatic decoding processes²². Finally, participants' attention was drawn to the eye region by displaying a pre-stimulus fixation point at the eye-level of the upcoming face stimulus. This feature of the task is particularly decisive for ASD participants who do not preferentially attend to social stimuli^{24,43}, such as the eyes^{24–26}, and may be at a disadvantage^{26–28} in emotion categorisation tasks where attention is not expressly drawn to them. Indeed, emotion recognition performance is positively related to attention to the eye-region²³, notably for negative emotions such as fearful and angry expressions, primarily expressed using the upper part of the face⁴⁴.

Under the specific experimental conditions used in our design, we found that gaze direction has a similar impact on performance in emotion categorisation in ASD and TD participants. Although overall performance was higher in the TD group, individuals with ASD were able to integrate co-emitted social signals of gaze and emotional expression to inform emotion decoding. A key innovation of this study was to reveal the mechanism that instantiates the contextual impact of gaze direction on emotion categorisation by fitting theoretical decision models to the behavioural data. It is indeed conceivable that participants with ASD reach a higher level of performance in the salient gaze-emotion conditions by resorting to underlying processes that are completely different

from those used by control participants. Critically, we found that the same mechanism was at play in the ASD and in the TD groups and that improved recognition accuracy for highly salient threat-signalling emotion-gaze combinations corresponded to a selective enhancement of perceptual sensitivity to these combinations of gaze and emotion. Thus, the present findings demonstrate that ASD adolescents are not only able to decode emotions but that they also automatically integrate contextual gaze while doing so.

The present study thus extends previous evidence of intact face processing⁴⁵ and intact prioritisation of salient social cues over less salient ones⁴⁶ in ASD, by demonstrating that adolescents with ASD rely on the same mechanism as TD adolescents to combine contextual social cues (here gaze direction) with facial displays of emotions as a function of their salience for the observer. Given that the brief and sudden fixation point at the eye region (which triggers attention) was one of the critical differences between the current study and previous studies where participants with ASD failed to integrate social cues, it is possible that diminished spontaneous attention to the eyes accounts for at least part of the atypicalities in emotion processing commonly reported in ASD. This view is also compatible with the idea that diminished automatic orientation to socially relevant signals is a core deficit in ASD²⁸ as well as with data demonstrating that the processing of socially relevant signals is intact under motivated conditions⁴⁷. Future work will therefore need to manipulate eye fixation directly in order to confirm whether this is indeed a key parameter guiding emotion categorisation in ASD. Since our sample size is relatively small, it will also be important to replicate this work and assess its generalizability to various subtypes of ASD. However, it is important to note that the effect we report here replicates what has already been described in a sample of 24 healthy adults¹¹, which suggests that our effect is robust.

To conclude, our results demonstrate not only that adolescents with ASD take into account contextual gaze information while processing emotional displays, but more importantly, even though their overall emotion recognition accuracy is lower than TD adolescents, that the same mechanism, *i.e.* increased perceptual sensitivity, underlies such contextual impact in both groups. These results suggest the possibility that significant difficulties in social interaction and communication seen in ASD may exist independently of their ability to process the social signals themselves. Future experiments should address whether, when decoding skills appear preserved, ASD's social difficulties are related to dysfunctions in the motivation mechanisms driving attention to socially relevant signals or to the mechanisms underlying the preparation of appropriate response behaviour to perceived social signals, both crucial to social interactions in daily life.

Methods

Participants. Twenty-four adolescents with ASD aged between 12 and 17 years old and 24 TD adolescents participated in this study. Adolescents in the ASD group were recruited from the University Hospital Robert Debré (Paris, France). Final diagnosis of ASD was based on DSM IV-TR⁴⁸ criteria and made by summing the information from the Autism Diagnostic Interview-Revised (ADI-R)⁴⁹, the Autism Diagnostic Observation Schedule (ADOS)⁵⁰ and data from clinical reports made by experts in the field. ASD participants' Intelligence Quotient (IQ) was assessed using the full Wechsler Intelligence Scale for Children version IV⁵¹ (WISC IV). They were also tested for normal visual acuity using the Freiburg Visual Acuity and Contrast Test⁵² (FrACT version 3.8.2). This test was adapted to the distance of 0.3 meters. Normal vision was ensured by a Snellen fraction of 0.3/0.3 (distance of test/distance at which the subject can identify the indicated symbol). Trait anxiety was assessed using an abbreviated form⁵³ of the State-Trait Anxiety Inventory⁵⁴ (STAI; See Table 1). Finally, no participants were on medication during the period of the study.

Adolescents in the TD group were recruited from a mainstream school. They did not report any history of developmental or other psychiatric illness. They all had normal or corrected to normal vision. Due to time constraints, IQ in the TD group was assessed with the French Wechsler Abbreviated Scale of Intelligence (four subsets) which has been found to be highly reliable in giving a representative score of the full IQ⁵⁵ in the general population (See Table 1).

The experimental protocol and associated methods were approved by INSERM and licensed by the local research ethics committee (ClinicalTrials.gov Identifier: NCT02628808, Protocol Study ID: 2008-A00019-46). Our study was performed in accordance with the Declaration of Helsinki. All parents and children provided written informed consent according to institutional guidelines of the local research ethics committee. All the participants were debriefed and thanked following their participation.

Materials and design. The stimuli consisted of 12 face identities (6 female) selected from the original set¹¹ of 36 identities. Two (1 female) additional identities were used during training only. The original identities were drawn from the Radboud Face Database⁵⁶ and were modified¹¹ using Adobe Photoshop CS5.1 (Adobe Systems, San Jose CA) and parametrically morphed¹¹ using FantaMorph (Abrosoft <http://www.fantamorph.com/>) so that, for each identity, 30 stimuli were created; 7 morphs (emotion intensities) * 2 emotions (fear/anger) * 2 gaze directions (direct/averted), plus two neutral stimuli, one with direct and one with averted gaze. Hence, our task included 360 trials, one third of original number of trials¹¹, divided into 3 blocks in order to avoid tiredness and inattention effects.

Emotion Categorisation Task. The experimental task was a two-choice emotion categorisation task (fear or anger). The stimuli were projected on a black background using Psychophysics-3 Toolbox^{57,58} of Matlab (version R2014a) software (<http://uk.mathworks.com/>). In each trial, participants saw a white oval line that remained throughout the trial to indicate the size and location of the upcoming stimulus. After 500 ms of the oval's appearance a fixation point appeared at the level of the stimulus' eyes for 1000 ms, followed by a target face presented for 250 ms. As soon as the face disappeared the participants had a 4000 ms response window to indicate if they thought the face expressed anger or fear. To do so, they pressed one of the two control buttons (Ctrl) on the keyboard. One button represented fear and the other anger. The side of the button corresponding to fear or

	ASD (n = 20)	TD (n = 20)	Test value, p value, effect size value
Age	14.10 (0.43)	13.75 (0.33)	U = 178.000, ASD = TD = 20, p = 0.543, r = 0.09
Gender	Males n = 16	Males n = 15	$\chi^2(1) = 0.143$, p = 0.705, $\phi = 0.06$.
IQ total	103.2 (4.3)	100.1 (2.1)	U = 184.500, ASD = TD = 20, p = 0.664, r = 0.07
IQ verbal	102.9 (5.6)	100.4 (2.2)	U = 189.500, ASD = TD = 20, p = 0.776, r = 0.04
IQ performance	104.8 (4.5)	99.65 (2.8)	U = 175.500, ASD = TD = 20, p = 0.507, r = 0.10
Anxiety	14.6 (0.9)	13.5 (0.7)	U = 162.000, ASD = TD = 20, p = 0.302, r = 0.16
Total non-response trials	32 (0.34)	54 (0.43)	U = 150.500, ASD = TD = 20, p = 0.164, r = 0.22
ADOS	11.4 (0.45)	NA	NA

Table 1. Mean (S.E.M.) of chronological age, gender, total IQ, verbal IQ, performance IQ and trait anxiety for both groups (after automatic matching procedure), total missed trials of each group and ADOS for the ASD group.

anger (e.g., Left Ctrl: anger, Right Ctrl: fear) was consistent across trials for each participant but counterbalanced between participants.

Go/no-Go Task. To control for potential overall RT differences between the two groups we measured their general reaction times (RTs). We systematically performed all RTs analyses without and with co-varying the general RTs out, and found that the results remain the same. Participants took part in a Go/no-Go task, created on E-prime stimulus presentation software (<http://www.pstnet.com/eprime.cfm>). They saw a white fixation cross on a grey background, in the centre of the screen, followed 67% of the time by a black dot. When the black dot appeared participants had to press the SPACE button as fast as possible.

Procedure. Participants were seated at 30 cm distance from the laptop. During the Emotion categorisation task, they were told that they would see faces at the centre of the screen and had to indicate whether they thought that the face expressed anger or fear by pressing the corresponding button. Initially, they completed 10 trials of the emotion categorisation task (training), in order to familiarise with the task. In order to avoid boredom and tiredness effects, the main task was divided in 3 blocks of 120 trials each. At the end of each block, participants could see their percentage of accuracy and speed of responding. Participants completed the first block of the task. Subsequently they did the Go/no-Go test and a second block of the main task. Following that, the participants gave their answers to the Anxiety scale verbally to the experimenter before they completed the third and final block of the emotion categorisation task. Finally, their visual acuity was tested.

Data Analysis. Four ASD and one TD participants were excluded because they were at chance level during the task (accuracy 40–60%) resulting in 20 ASD participants. These 20 ASD participants were then automatically matched, using R Project for Statistical Computing (www.rproject.org) with 20 TD participants (among 23) according to chronological age, gender and IQ (see Table 1). The matched 20 TD and 20 ASD participants had the same levels of anxiety, which is the most prevalent disorder comorbid with ASD⁵⁹ and has been found to increase one's sensitivity to social threat⁶⁰ (see Table 1). ADOS scores of the ASD group which were not measured with module 4 (n = 1) were calibrated⁶¹ and descriptive values can be found in Table 1. Analyses were performed only on valid (response) trials. All non-response trials and all trials with RTs less than 200 ms were excluded from the analysis. Lastly, we compared the total number of non-response trials between the two groups and found no significant differences (see Table 1).

Model-free analyses on performance. Mean emotion accuracy, as well as the standard error of the mean (S.E.M) for each group are listed in Table 2. RTs descriptive values and results can be found Table 3. Data was analysed using Matlab software and SPSS-18. All p-values reported are two-tailed. Partial eta squared (η_p^2) is reported as the effect size of the F statistics, r of the non-parametric comparisons and phi (ϕ) for the chi squared test on gender. A value of $\eta_p^2 = 0.01/r = 0.1/\phi = 0.1$ represents a small effect size, $\eta_p^2 = 0.06/r = 0.3/\phi = 0.3$ a medium one and over $\eta_p^2 = 0.14/r = 0.5/\phi = 0.5$ a large effect size⁶².

We first performed a $2 \times 2 \times 7$ repeated measures ANOVA on accuracy with Emotion (anger vs. fear), Gaze (direct vs. averted) and Intensity (7 levels) as within subjects' factors and Group (ASD vs. TD) as a between subject factor. The same analysis was performed within each group independently. As the distribution of the TD group's residuals was not normal, post-hoc analyses are done using non-parametric statistical tests. In order to compare the performance of each group in highly salient emotion-gaze combinations (Threat+) as compared to less salient emotion-gaze combinations (Threat-), we calculated the mean for each of these two types of combinations.

Further, we calculated the difference between these two means and used it to compute the Bayes factor⁶³ for the difference between these two conditions in the ASD group. A Bayes factor uses prior knowledge in association with newly acquired data to describe the likelihood (llh) of the current data in supporting an alternative

	Conditions:	Anger-Averted	Anger-Direct	Fear-Averted	Fear-Direct	Overall
ASD	Accuracy (%)	76 (2)	79 (2)	86 (3)	85 (2)	82 (2)
TD	Accuracy (%)	80 (2)	87 (2)	88 (8)	90 (7)	86 (6)

Table 2. Mean (S.E.M.) of emotion accuracy per group per condition.

	Conditions:	Anger-Averted	Anger-Direct	Fear-Averted	Fear-Direct	Overall
ASD	RTs (ms)	866 (38)	841 (36)	855 (40)	869 (38)	858 (37)
TD	RTs (ms)	1046 (37)	1021 (33)	1073 (35)	1036 (39)	1044 (34)

Table 3. Mean (S.E.M.) of RTs per group per condition.

hypothesis (H1) against a null (H0) and is given by the formula $B = \ln h_{H1} / \ln h_{H0}$. If the Bayes factor is above 3 then the data provides support for the H1 while if it is less than 1/3 it provides support for the H0. We wanted to test the H1 that there is a significant difference between Threat+ and Threat− in the ASD group against an H0 that finds no difference between the conditions and for this purpose we used the TD group's mean difference as the prior.

Model selection. We used model based analyses to characterise the mechanisms underlying the enhanced performance of the groups in the Threat+ combinations, compared to the Threat− combinations, in the framework of Signal Detection Theory (SDT)³⁴. Participants' behaviour was accounted for using a simple psychometric model:

$$p(\text{anger}) = \Phi(w * x + b) \quad (1)$$

where $p(\text{anger})$ is the probability of selecting the emotion of anger, Φ is the cumulative normal function and x is the evidence for the corresponding emotion (emotion intensity; from -7 corresponding to intense fear, to $+7$ corresponding to intense anger, through 0 which represents a neutral expression), w to the perceptual sensitivity to the emotional expression (*multiplicative* by the sensory evidence), and b to an *additive* stimulus-independent bias toward 'anger' or 'fear' responses.

We compared two models that could account for the influence of gaze on emotion categorization: model 1, where gaze direction would bias responses towards Threat+ combinations and model 2, where gaze direction would enhance perceptual sensitivity to Threat+ combinations.

A change in the decision bias implies that the bias toward anger or fear is different for direct and averted gaze conditions such as:

$$p(A|\text{dir}) = \Phi(w * x + b_{\text{dir}}) \quad (2)$$

$$p(A|\text{avt}) = \Phi(w * x + b_{\text{avt}}) \quad (3)$$

where the probability of selecting the emotion of anger is $p(A|\text{dir})$ in the direct gaze condition and $p(A|\text{avt})$ in the averted gaze condition, w is the perceptual sensitivity to the emotional expression (common to all conditions if the effect is on the bias), b_{dir} is a bias toward 'anger' or 'fear' responses in the direct gaze condition, that is different from b_{avt} , the bias toward 'anger' or 'fear' responses in the averted gaze condition.

A change on the sensitivity implies that the sensitivity is shared for THREAT+ conditions (Anger direct and fear averted) and different from the sensitivity to THREAT− conditions (Anger averted and fear direct) such as:

$$p(A|\text{Th+}) = \Phi(w_{\text{th+}} * x + b) \quad (4)$$

$$p(A|\text{Th-}) = \Phi(w_{\text{th-}} * x + b) \quad (5)$$

where the probability of selecting the emotion of anger is $p(A|\text{Th+})$ in Threat+ condition and $p(A|\text{Th-})$ in Threat− condition, $w_{\text{th+}}$ is the perceptual sensitivity to the emotional expression in Threat+ conditions, $w_{\text{th-}}$ is the perceptual sensitivity to the emotional expression in Threat− conditions, and b is a bias toward 'anger' or 'fear' responses (common to all conditions if the effect is on the sensitivity).

We used Bayesian model selection and calculated the Bayesian information criterion (BIC) to determine which of the two models was more likely to explain the observed data. To check whether TD and ASD participants showed differences in the underlying model best fitting their behaviour (increased performance for Threat+ conditions, which could be due either to changes in sensitivity or decision bias), we applied fixed-effects model comparisons. These comparisons assume that all participants within one group used the same underlying model to generate their behaviour. To compare the two models within each group, we computed the Bayes factor⁶⁴ of the different models as the ratio of each model's evidence to the compared model's evidence. To compare sensitivity parameter estimates across Threat+ and Threat− conditions within each group, we computed the marginal posterior probability density function (pdf) of the sensitivity parameter in each condition in 0.01 steps;

and computed the empirical probability that the sensitivity parameter in the Threat+ condition is higher than the sensitivity parameter in the Threat− condition (by computing the posterior pdf of the difference in sensitivity parameter between the two conditions, and taking the area under the curve above zero). Importantly, this statistic is independent of the shape of the distribution, but given the approximate Gaussian shape of the difference in sensitivity parameter between conditions, we report standardized effect sizes within each group corresponding to the ratio between the best-fitting mean of the difference divided by the best-fitting standard deviation of the difference (in a least-squares sense).

Analyses on reaction times. We finally conducted a $2 \times 2 \times 7$ repeated measures ANOVA on reaction times (RTs) with Emotion (anger vs fear), Gaze (direct vs averted) and Intensity (7 levels) as within subjects' factors and, Group (ASD vs. TD) as a between subject factor (for descriptive values see Table 3).

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Author Contributions

C.I., M.E.Z., V.W., C.C. and J.G. designed the study. C.I. conducted the experiment. C.I., M.E.Z. and V.W. performed data analysis and model selection. C.I., M.E.Z., C.C. and J.G. prepared the manuscript. I.S., F.A. and R.D. conducted the patients' clinical evaluations. All authors reviewed and approved the final manuscript.

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Chapter 2 conclusion

In chapter 2, I presented the evidence for contextual effects on emotion processing in both neurotypical and ASD individuals. I, then, presented the first experiment of this Ph.D. which investigated the processing of social threats in adolescents with and without ASD, after implementation of a fixation jitter at the level of the stimulus' eye-region (motivating condition).

The main messages of experiment 1 are the following: 1) adolescents with ASD show reduced emotion recognition accuracy for anger and fear in comparison to a well-matched group of TD adolescents, although the accuracy of both groups was well above chance, 2) gaze direction impacted on the processing of social threats in both groups similarly in a way that anger paired with direct gaze and fear paired with averted gaze were more accurately recognised than the opposite combinations and 3) the mechanism behind the impact of gaze direction on the categorisation of social threats was the same between groups and the same with the mechanism found in neurotypical adults, using the same experimental task (El Zein et al., 2015); gaze direction enhanced participants' perceptual sensitivity to salient combinations of threat.

Adolescents with ASD are able to process facial expressions of threat, those being anger and fear, of variable intensity and this processing is influenced by the concomitant gaze direction. The question still remains whether adolescents with ASD can use task-irrelevant facial expressions of threat in order to adapt their behaviour when their emotion processing abilities are preserved.

Chapter 3: Adaptive responses to social threats in autism spectrum disorders

In this chapter, I will present the second experiment of my Ph.D., which investigates whether, when emotion processing abilities are preserved, adolescents with ASD use threatening emotions emitted by another to adapt their behaviour. Within a context of implicit social threat, can adolescents with ASD use task-irrelevant displays of anger and fear in order to regulate their behaviour?

In chapter 1, I described how the literature behind emotion processing is mixed and the performance of the ASD group depends on methodological factors. In chapter 2, by taking into account these methodological factors, we demonstrated accurate processing of facial expressions of anger and fear in adolescents with ASD, regardless of an overall reduced decoding accuracy in ASD as compared to the TD group. Consistent with our findings, recent work (Chevallier et al., 2013 for details see section 1.4.2) found that under specific conditions individuals with ASD can cognitively process socially salient information, which in turn impact on their performance. Our findings in experiment 1 suggest that diminished social orientation, an aspect of reduced social interest in ASD, cannot stem from deficits in the processing of emotional signals of threat given that when this was targeted by attention orienting to the eyes of the stimulus, adolescents with ASD processed threatening emotions accurately.

Extensive reviews of the literature propose that individuals with ASD might not only extract and process emotional signals differently than TD individuals but they could also differ in the preparation and regulation of adaptive responses to those signals (Gaigg, 2012; Harms et al., 2010; Loveland, 2005; Loveland, 2001). This is not surprising because it stresses the intimate link between perception and action as described in chapter 1. Individuals with ASD are characterised by “a pervasive lack of responsiveness to others” and “marked impairments in the *use* of multiple nonverbal behaviours, such as eye to-eye gaze, facial expression, [...] to *regulate* social interactions” (American Psychiatric Association, 1994, 2000). Gaigg, (2012) reports that “they also make fewer attempts to initiate emotional exchanges and together these differences afford autistic individuals fewer opportunities [...] to learn about the hedonic significance of environmental stimuli through them”. If they have fewer opportunities to learn about the hedonic experience of stimuli they also have fewer opportunities to learn about the aversive experience of such stimuli, which is highly relevant in the context of social threats. Importantly, such difficulties in regulating socio-emotional exchanges cannot be attributed to deficits in the perceptual processing and understanding of others’ socially relevant signals (Dinstein et al., 2010). Indeed under motivated conditions, where attention to the stimuli is maximised, adolescents with ASD can detect, process and interpret these signals accurately, whether these depict biological

motion (Cusack, Williams, & Neri, 2015), direct gaze (Chevallier et al., 2013) or emotions (see section 2.3: Ioannou et al., 2017). Given these functionally intact signals from the perceptual system in response to relevant social stimuli, deficits in this group could rather result from maladaptive responses to those signals.

Adaptive regulation of one's behaviour in response to relevant social stimuli requires comprehension of their meaning or what they afford behaviourally and individuals with ASD might lack the ability to infer or understand the meaning of social threats. Grèzes, Wicker, Berthoz, & de Gelder, (2009) showed adults with and without ASD static and dynamic presentations of actions which had or not an emotional meaning; people either opened a door while staring straight ahead in the neutral condition or opened the door and faced a threat in the fear condition. During exposure to the emotional gestures and regardless of presentation mode both groups activated the superior temporal sulcus which is involved in visual processing. Importantly, control participants also activated emotion processing related brain areas, namely the amygdala, the lateral inferior frontal gyrus (IFG) and the dorsal PM, but the same was not the case for the ASD group. Lastly, the ASD group showed reduced activity within the amygdala and dorsal PM as well as atypical influence of the former on the latter. The amygdala is not only involved in the processing of biologically salient stimuli as explained in section 1.3.4 but via its connections to the dorsal PM cortex, it also plays a crucial role in the initiation of adaptive responses in non-human primates (Amaral & Price, 1984; Avendaño, Price, & Amaral, 1983). Lesions in this area can disrupt the perception of threat and fear responses to this threat in non-human primates (Bauman, Lavenex, Mason, Capitanio, & Amaral, 2004). Individuals with ASD show abnormal activation of the amygdala but demonstrate accurate processing of threat signals (see section 2.3). Taken together, these findings point to a potential inability of individuals with ASD to grasp the emotional meaning of actions for the preparation and initiation of behavioural responses to social threats.

3.1 Adolescents with autism can use implicit social threat to adapt their behaviour

(Experiment 2)

This experiment will be presented as the manuscript of the scientific article in preparation. The supplementary material can be found in Appendix 1 and the analysis of the temporal dynamics of the participants' movement kinematics in Appendix 2. Although the results were not significant, it is important to show that the behaviour between groups is comparable. The pupil data processing and the methodological reasons for its exclusion from the final manuscript can be found in Appendix 3.

Experiment 2: in preparation for submission at Scientific Reports.

Adolescents with autism can use implicit social threat to adapt their behaviour

Adolescents with autism can use implicit social threat to adapt their behaviour

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Abstract

Socio-communicative difficulties in autism spectrum disorders (ASD) have been investigated for years and the roots of these difficulties remain unclear. Inconsistencies in the results from emotion categorization tasks suggest that a generalized emotion processing impairment is unlikely to be the primary deficit in ASD, and that socio-communicative difficulties might exist independently of the ability to decode social signals. In this paper, we go a step further by testing the hypothesis that observed social difficulties in ASD are the consequence of a deficit in adapting and regulating behaviour in response to emotional signals. To do so, 28 ASD and 28 matched controls performed a free action choice task in the presence of task-irrelevant threat-related emotional displays and an emotion categorisation task. The results revealed that TD and ASD adolescents adopted overall similar behaviours in the presence of task-irrelevant emotional displays: they chose actions that allowed them to avoid angry individuals more often and had longer reaction times to approach than to avoid fearful individuals. Furthermore, similarly to TD controls, ASD adolescents categorized emotional displays as fear or anger accurately. We discussed these findings in relation to the theories favouring preserved processing of social cues in ASD.

Introduction

Autism spectrum disorders (ASD) are neurodevelopmental conditions, characterised by deficits in communication and reciprocal social interaction manifested alongside repetitive patterns of behaviour and restricted interests (American Psychiatric Association, 2013). Individuals with ASD present prominent difficulties in the perception of emotional signals compared to typically developing (TD) individuals and the roots of these difficulties remain unclear. The most dominant account suggests that deficits in emotion processing (Corbett et al., 2009; Harms et al., 2010; Hobson, 2005) underlies the persistent failures in emotion recognition tasks (Harms et al., 2010; Loveland, 2001; Uljarevic & Hamilton, 2013) in ASD. However, a number of studies (Blair, 2003; Ioannou et al., 2017; Jones et al., 2011; Ozonoff et al., 1990), including studies involving large samples of well-matched participants, find no difference between TD and ASD individuals in the perception of facial affect. For example, by implementing a pre-stimulus fixation to the stimulus' eye-region, we recently demonstrated (Ioannou et al., 2017) that adolescents with ASD can accurately process emotional displays of threat while taking into account concomitant, task-irrelevant gaze direction. Importantly, using computational modelling of participants' behaviour we revealed that the same mechanism, i.e. increased perceptual sensitivity, underlies the contextual impact of gaze in both groups. This suggests that a generalized emotion processing impairment is not likely to be the primary deficit in ASD (Ozonoff et al., 1990) and that socio-communicative difficulties might exist independently of the ability to decode social signals. In this paper, we go a step further by testing the hypothesis that observed social difficulties in ASD are the consequence of a deficit in regulating behaviour in response to emotional signals (Bachevalier & Loveland, 2006; Gaigg, 2012; Loveland, 2005; Loveland, 2001).

This behavioural self-regulation hypothesis (Hellendoorn, 2014; Loveland, 2001), builds on the concept of affordances (Gibson, 1979), which characterises the possibilities for action offered by the physical and social environment (Zebrowitz-McArthur & Baron, 1983) as a function of the capabilities of the observer. In other words, observers do not simply decode emotional signals, they adapt their behaviour according to others' emotional signals. Being able to process an emotional signal would indeed be of little use if one was unable to understand what it affords behaviourally (Gaigg, 2012). Evolutionary accounts of emotional displays have convincingly argued that the very function of emotions is to serve communication purposes by conveying critical information about the emitters (Fridlund, 1994; Keltner & Haidt, 1999) and by prompting behavioural responses in the observers (Dezecache et al., 2013). Based on these theories, interpersonal contexts (Hobson, 2012; Loveland, 2005) are of key importance to reveal the mechanisms underlying the processing of social cues and the mechanisms behind the regulation of appropriate responses.

Vilarem et al., (under review) created an original setting assessing two things: 1) the impact of emotional displays on action-related decisions and 2) explicit emotion categorisation. In the free action choice phase, participants' had to choose between competing affordances in a realistic context: participants were asked where they would prefer to sit in a waiting room furnished with four chairs; the two outer seats were free and the two middle seats were occupied by individuals displaying a neutral facial expression or an expression of fear or anger (Figure 1). Participants avoided anger and made quicker movements when approaching fearful individuals, which suggests that facial displays of anger and fear prompt action tendencies that are congruent with their social function. Angry faces favour avoidance behaviour, in agreement with the fact that they enhance cues of strength (Sell et al., 2014) and signal an impending aggression of the observer (Sander et al., 2007); fearful faces enhance cues of vulnerability and affiliation (Hammer & Marsh, 2015) and prompt prosocial- approach behaviours. In the explicit emotion categorisation phase, participants were asked to categorise the emotion as fear or anger. Importantly, participants' ability to explicitly process emotions did not correlate with their ability to adapt their behaviour during the action regulation phase. This suggests that the underlying mechanisms for action decision and emotion categorisation are independent and that the tasks are successful in dissociating them.

Here, we were thus interested in using these two tasks to compare TD adolescents and adolescents with ASD in order to find out whether individuals with ASD detect emotions as communicative signals and adapt their behaviour accordingly. We used an adapted version of the above described protocol (free action choice task and emotion categorisation task). In typical individuals, behavioural responses to others' emotions are negatively related to the individual's autistic traits, such that people with higher autistic traits are less responsive than those with lower autistic traits (Meng et al., 2017). Only few studies in ASD research have investigated behavioural responses to affective and socially demanding interactions, such as a tea party or a social gathering where the experimenters emotionally react to situational factors (e.g. hurt themselves or lose their wallet). These studies report intact basic responses to emotional signals in ASD (Blair, 2003), that is physiological arousal in response to others' distress in the absence of behavioural responses (Blair, 1999) and intact behavioural responses to anger (Klapwijk et al., 2017), which is a clear social threat signalling a violation of social rules/expectations (Averill, 1982). However, they do not show anticipatory concern (J. A. Hobson et al., 2009) or heart rate changes (Corona et al., 1998) and they generally demonstrate reduced empathic/affiliative *behavioural* responses to others' signals of distress (Bacon et al., 1998; Blair, 2003; Loveland & Tunali, 1991; Yirmiya et al., 1992). Our paradigm is different from previous ones in that it recreates a realistic interactive environment, which provides action possibilities in the absence of explicit social demands. Given the above and under those experimental conditions, we predicted that: 1) individuals with ASD will adapt

their behaviour to angry faces by avoiding them but 2) they will either show no preference between approaching and avoiding fear or they will avoid it similarly to anger, because it is an arousing negative emotion that signals the presence of a potential danger in the environment (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003).

Results

Task 1: Impact of emotional displays on free action choices

The experimental task was a free action-choice task, during which participants faced a visual scene representing a waiting room with four chairs, where the two middle seats were occupied by two individuals. One of the two individuals always displayed a neutral facial expression while the other displayed either a neutral, angry or fearful facial expression, the last two of varying intensity (4 levels of emotion strength). In each trial, participants were requested to choose where they would like to sit by directing the mouse cursor toward one of the two available outer seats, as accurately and as quickly as possible. Participants were explicitly informed that there were no correct choices in this task. They were informed however that they needed to correctly perform their movement for their response to be registered (see method for details). Importantly, participants were trained exclusively with neutral stimuli, had to fixate a central fixation cross throughout each trial, and the presence of emotional expressions was never mentioned to them. When choosing one of the two available outer seats, participants chose to sit either next to the neutral (referred to as “Away”: away of the emotional actor) or the emotional actor (“Toward”: toward the emotional actor). Given the two emotions and the two sides, four conditions of interest arise: anger-away (AA), anger-toward (AT), fear-away (FA), fear-toward (FT).

Insert Figure 1 here

Performance across blocks. Participants completed a total of 240 trials in 4 blocks of 60 trials each. We first ran an ANOVA to investigate potential effects of blocks on participant’s proportion of correct movements, and found a main effect of blocks ($F(3,162) = 5.517, p = .005$ Greenhouse-Geisser corrected, $\eta_p^2 = .093$), suggesting that the proportion of correct movements increased over time, potentially as a result of learning. There was a main effect of group ($F(1,54) = 5.314, p = .025, \eta_p^2 = .09$), related to better overall performance in the ASD group (mean = 80%; S.E.M. = 1.1) than in the TD group (mean = 73%; S.E.M. = 1.3) but no interaction between block and group was revealed ($F(3,162) = 0.495, p = .619$ Greenhouse-Geisser corrected, $\eta_p^2 = .009$). Within-group analysis indeed showed that the proportion of correct movements increased over blocks in the ASD group ($F(3,81) = 3.245, p = .049$ Greenhouse-Geisser corrected, $\eta_p^2 = .107$) and at a trend level in the TD group ($F(3,81) = 2.759, p = .067$ Greenhouse-Geisser corrected, $\eta_p^2 = .093$).

Overall tendency to go away from the emotional displays. Overall, participants showed a tendency to select the seat next to the neutral actor and away from the emotional actor more compared to the seat next and toward the emotional actor (Effect of side: $F(1,54) = 6.029, p = .017, \eta_p^2 = .10$). This tendency

did not differ between the groups (Side*Group: $F(1,54) = 0.684$, $p = .412$, $\eta_p^2 = .013$). However, it varied as a function of the emotion's intensity (Side*Intensity: $F(3,162) = 3.004$, $p = .032$, $\eta_p^2 = .053$) and this differed between groups at trend level (Side*Intensity*Group: $F(3,162) = 2.236$, $p = .086$, $\eta_p^2 = .04$). Within-group analyses revealed that while the ASD group showed an overall tendency to avoid the emotional actor irrespective of the intensity of the emotional displays (Effect of side: $F(1,27) = 4.007$, $p = .055$, $\eta_p^2 = .129$; Side*Intensity: $F(3,81) = 2.076$, $p = .127$ Greenhouse-Geisser corrected, $\eta_p^2 = .071$), this avoidance strategy increased with emotion intensity in the TD group (Effect of side: $F(1,27) = 2.022$, $p = .166$, $\eta_p^2 = .07$; Side*Intensity: $F(3,81) = 3.131$, $p = .03$, $\eta_p^2 = .104$).

Specific impact of task-irrelevant emotional displays on action choices in both TD and ASD adolescents. Importantly, we observed that the nature of the emotion in the scene influenced participants' action choices differently (Emotion*Side interaction: $F(1,54) = 6.361$, $p = .015$, $\eta_p^2 = .105$) and this varied as a function of the emotion's intensity (Emotion*Side*Intensity interaction: $F(3,162) = 4.283$, $p = .006$, $\eta_p^2 = .073$). Participants chose to move away from angry actors more often than they chose to move towards them ($t(55) = 3.381$, $p = .001$, $d = .45$) but no such difference was observed in the case of fear ($t(55) = 0.133$, $p = .895$, $d = .02$) where participants seemed indifferent to sitting toward or away from it.

Neither of these interactions differed between the groups (Emotion*Side*Group: $F(1,54) = 0.942$, $p = .336$, $\eta_p^2 = .017$; Emotion*Side*Intensity*Group: $F(3,162) = 1.317$, $p = .271$, $\eta_p^2 = .024$), but given our specific a priori hypotheses for differential behaviours between TD and ASD when facing anger and fear displays, we ran within group analyses. These revealed that these interactions were only significant in the TD group (Emotion*Side: $F(1,27) = 4.281$, $p = .048$, $\eta_p^2 = .137$; Emotion*Side*Intensity: $F(3,81) = 4.012$, $p = .01$, $\eta_p^2 = .129$) and not in the ASD group (Emotion*Side: $F(1,27) = 2.092$, $p = .16$, $\eta_p^2 = .072$; Emotion*Side*Intensity: $F(3,81) = 1.239$, $p = .301$, $\eta_p^2 = .044$). Yet, within-group comparisons between our four conditions of interest showed a significant tendency to move away from angry actors more often than to move towards them in both groups (TD: $t(27) = 2.396$, $p = .024$, $d = .45$; ASD $t(27) = 2.342$, $p = .027$, $d = .44$), and no significant difference between avoiding and approaching fear in either group (TD: $t(27) = -0.845$, $p = .405$, $d = .16$; ASD: $t(27) = 1.04$, $p = .308$, $d = .2$). The TD group also indicated a preference to approach fear as compared to anger (TD: $t(27) = 2.285$, $p = .03$, $d = .43$; ASD $t(27) = 1.385$, $p = .177$, $d = .26$) but anger and fear were avoided to a similar extent by both groups (TD: $t(27) = 1.682$, $p = .104$, $d = .32$; ASD: $t(27) = 1.327$, $p = .196$, $d = .25$).

Given our insignificant interaction in the ASD group and the fact that we have a prior for the choice behaviour from an adult group, we computed the Bayes factor to test the strength and validity of the difference on the proportion of choices between the two parts of the interaction (see method for details) in both groups - TD and ASD adolescents - as compared to neurotypical adults (Vilarem et al.,

under review) and next in ASD adolescents as compared to the TD ones. We found a Bayes factor greater than 3 when we compared this difference in TD (Bayes factor = 4.8) to previously tested neurotypical adults, confirming an overall increase in the same way as in neurotypical adults. The same was not true for the ASD group when compared to neurotypical adults (Bayes factor = 1.4) or TD controls (Bayes factor = 1.4). A value between 1/3 and 3 does not allow for either accepting or rejecting our hypothesis for a significant interaction in the ASD group, as would be expected from the TD adolescents group or previous neurotypical adult data (Vilarem et al., under review).

Insert Figure 2 here

Analyses of proportion of choice were repeated while covarying participants' autistic traits score, as measured by the Autism Symptom SELF-Report³¹ (ASSERT; see Method for details) and the results were the same (see Supplementary Data for results).

Overall shorter reaction times in TD adolescents compared to adolescents with ASD and longer reaction times when approaching fear. The TD group (M = 427, S.E.M. = 9.3) was overall quicker in responding than the ASD group (M = 493, S.E.M. = 9.1) (Effect of group: $F(1,54) = 7.582$, $p = .008$, $\eta_p^2 = .123$). There was a trend for an Emotion*Side interaction on participants' RTs (Figure 3A: $F(1,54) = 4.839$, $p = .032$, $\eta_p^2 = .082$) such that participants were quicker to avoid fearful actors than to approach them ($t(55) = -1.779$, $p = .081$, $d = .24$). This interaction did not significantly differ as a function of the emotion's intensity (Emotion*Side*Intensity interaction: $F(3,162) = 0.427$, $p = .734$, $\eta_p^2 = .008$), nor between groups (Emotion*Side*Group = $F(1,54) = 0.204$, $p = .653$, $\eta_p^2 = .004$). Again given our specific a priori hypotheses for anger and fear displays, we ran within group analyses: neither the Emotion*Side interaction was significant (Figure 3B TD: Emotion*Side: $F(1,27) = 2.907$, $p = .100$, $\eta_p^2 = .097$; Figure 3C ASD: Emotion*Side: $F(1,27) = 1.932$, $p = .176$, $\eta_p^2 = .067$), nor the RT difference between approaching and avoiding fear (TD: $t(27) = -1.465$, $p = .155$, $d = .28$; ASD: $t(27) = -1.025$, $p = .315$, $d = .19$). Only a significant effect of intensity in the TD group was observed ($F(3,81) = 3.176$, $p = .028$, $\eta_p^2 = .105$), with TD participants becoming significantly quicker when the emotion was of 100% strength (level 3 vs level 4: $t(27) = 2.557$, $p = .017$, $d = .48$). No other effect or interaction was significant in either group (all $p \geq 0.1$).

Insert Figure 3 here

Analyses of RTs were repeated while co-varying out participants' autistic traits score, as measured by ASSERT and the results were the same (see Method for details and Supplementary Data for results).

Task 2: Explicit emotion categorisation task.

The goal of this task was to assess participants' abilities to explicitly recognize emotions that are presented in their peripheral vision. Participants were requested to determine whether one of the actor present in the same emotional scenes as in Task 1 expressed fear or anger, using a scale ranging from intense anger to intense fear (see methods for details).

Accuracy above chance in both TD and ASD group. The results showed that both the TD (M = 67%; S.E.M. = 2.2) and ASD (M = 64%; S.E.M. = 2.9) adolescents scored above chance (Figure 4A; TD: $t(23) = 7.668$, $p < .001$, $d = 1.6$; ASD: $t(26) = 4.718$, $p < .001$, $d = .9$) and there was no difference in overall emotion accuracy between the groups (Effect of group: $F(1,49) = 0.678$, $p = .414$, $\eta_p^2 = .014$). There was a strong Emotion*Group interaction ($F(1,49) = 7.478$, $p = .009$, $\eta_p^2 = .132$), related to the fact that TD adolescents recognized fear better than anger (Effect of emotion, TD: $F(1,23) = 6.875$, $p = .015$, $\eta_p^2 = .230$; ASD: $F(1,26) = 0.552$, $p = .464$, $\eta_p^2 = .021$).

Regarding the intensity ratings, there was an Emotion*Intensity interaction ($F(3,147) = 56.417$, $p < .001$, $\eta_p^2 = .535$ Greenhouse-Geisser correction) but there was no interaction with Group ($F(3,147) = 0.586$, $p = .537$, $\eta_p^2 = .012$ Greenhouse-Geisser correction): the subjective ratings of the intensity increased with the objective intensity of the emotional display, in both groups.

Insert Figure 4 here

Finally, to determine whether the ability to explicitly process emotions relates to the ability to use task-irrelevant emotions to make free action choice, we ran correlations between the participant's mean emotion accuracy measured in task 2 and the interaction value of their proportion of choice measured in Task 1. We found no relationship between explicit emotion recognition and participants' interaction value both in the TD group ($R = .031$, $p = .886$) and in the ASD group ($R = .044$, $p = .828$). This suggests that the mechanisms behind such abilities are different.

Discussion

The present experiment aimed to test whether socio-communicative difficulties in adolescents with ASD exist independently of their ability to decode social signals and whether they are related to a deficit in adapting and regulating response to emotional signals. The results showed that, besides some differences between the groups (increased avoidance for emotional displays of higher intensity and quicker RTs for TD participants), TD and ASD adolescents adopted overall similar behaviours in the presence of task-irrelevant emotional displays: they chose actions that allowed them to avoid angry individuals more often and had longer reaction times to approach than to avoid fearful individuals. Furthermore, similarly to TD controls, ASD adolescents categorized emotional displays as fear or anger accurately. No correlation between emotion categorisation and action decision performances was found, which suggests that our tasks tapped distinct mechanisms. These findings stand in contrast with behavioural self-regulation accounts (Hellendoorn, 2014; Loveland, 2001) that suggest that socio-communicative difficulties in individuals with ASD stem either from a deficit in processing of emotional signals and/or from a deficit in the mechanisms responsible for the preparation of adaptive responses.

Our results are in line with previous work in our team (Ioannou et al., 2017) showing that adolescents with ASD are able to decode facial expressions of threat while integrating concomitant gaze direction and that the mechanism behind this integration was the same. In the present paper, both groups recognised anger and fear well above chance in the explicit categorisation task confirming that ASD participants' emotion decoding abilities were preserved. Moreover, participants with ASD as TD controls were able to select an appropriate course of action and avoid the angry actor in the scene. Thus, adolescents with ASD demonstrated that they can decode emotions and regulate their behaviour adaptively in response to direct social threats.

More specifically, we found that both groups avoided anger, which signals aggression (Sander et al., 2007) and strength (Sell et al., 2014), demonstrating intact basic, evolutionary responses to threat. Importantly, the lack of behavioural preference for approaching or avoiding fearful individuals was the same in adolescents (ASD and TD groups) and in an adult group previously tested with the same paradigm (Vilarem et al., under review). Yet, although in the original study the analysis of the movement kinematics revealed a speed advantage (increased velocity) when approaching the fearful actor, our reaction times results indicate the opposite. Both groups took longer time to approach fear as opposed to avoiding it. Critically here, although it is assumed that affordances are directly perceived, this does not mean that people perceive and act upon all affordances (Hellendoorn, 2014). Rather, their perception depends on the abilities and characteristics of the observer, the nature of the information which is selected by the observer (e.g., perceptual system, central nervous system) and the observer's

interaction with the environment (Gibson & Pick, 2000; Hellendoorn, 2014). Thus, an important determinant of affordances and specifically in this case of what the social world affords for the individual is the individual themselves.

Adolescence is a distinct developmental period and thus what is afforded behaviourally at this stage by a fearful actor might be distinct from what is afforded behaviourally by the same stimuli at other stages in life. During adolescence the processing of ambiguous social threats – those could be neutral stimuli or in our case fearful stimuli which do not signal a direct threat, but rather an overall threatening environment (Taylor & Barton, 2015) and do not induce distinct behavioural action tendencies (Vilarem et al., under review) – is prone to developmental changes, while the processing of direct threats, i.e. anger, seems to be constant (Forbes, Phillips, Silk, Ryan, & Dahl, 2011). Adolescence is a period characterised by enhanced reactivity to threat (Hare et al., 2008), which could explain the overall tendency to avoid the emotional agents in both groups and could suggest that larger RTs when approaching fear might underline a decision that otherwise would not be prioritised. Overall our results cannot support claims that adolescents with ASD fail to perceive their emotional environment (Loveland, 1991), or that they fail to respond to that environment.

To conclude, our results demonstrate that adolescents with ASD can process facial signals of threat and use them in the same way as TD controls in order to regulate adaptive responses. Although both groups showed a clear tendency to avoid anger, none of the groups showed a tendency to approach fear as compared to avoiding it. The cases where they did approach fear were characterised by delayed RTs. Adolescence is a distinct developmental period characterised by enhanced reactivity to threat and differential brain responses to ambiguous threat, which could explain why contrary to adults, who show a dissociation in the action tendencies induced in them in response to anger and fear, here both groups preferred to generally avoid the emotional agents. These findings suggest that the mechanism behind the preparation of avoidance responses in response to threat is intact in ASD. Future studies should tackle the responses of individuals with ASD to clearly pro-social emotions, such as happiness, which are affiliative and crucial for the establishment of every day social interactions.

Method

Participants. Thirty-four TD adolescents and thirty adolescents with ASD, aged between 12 and 17 years old, took part in this study. The ASD group was recruited from the University Hospital Robert Debré (Paris, France). None of the participants was on medication during the period of the study, diagnosis was based on reports by expert clinicians according to DSM IV-TR (APA, 1994) criteria, and on scores on the Autism Diagnostic Interview-Revised (ADI-R)(Lord, Rutter, & Couteur, 1994) and on the module 4 of the Autism Diagnostic Observation Schedule (ADOS)(Lord et al., 2000). The ADI scores, the total ADOS score, the ADOS social subscales (communication: ADOS_{com}; reciprocal social interaction – RSI: ADOS_{RSI}) that determine the total ADOS score, and the non-social subscales scores (imagination: ADOS_{imag}; stereotyped behaviours and restricted interests: ADOS_{ster}) are reported in Table 1. ASD participants' Intelligence Quotient (IQ; Table 1) was assessed using the full Wechsler Intelligence Scale for Children version IV (WISC-IV)(Wechsler, 2003). The TD group was recruited from a mainstream school. Participants did not report any history of developmental or other psychiatric illness. Due to time constraints, the IQ of the TD group was assessed using the French Wechsler Abbreviated Scale of Intelligence, which includes four subsets of the original WISC-IV and is reliable in giving a representative score of the full IQ (Grégoire, 2009) in the general population (Table 1).

Insert Table 1 here

Both groups were tested for normal visual acuity using the Freiburg Visual Acuity and Contrast Test (Michael Bach, 1996) (FrACT version 3.8.2) which was adapted to the distance of 0.4 meters. Normal vision was ensured by a Snellen fraction of 0.4/0.4 (distance of test/distance at which the subject can identify the indicated symbol). Furthermore, all participants completed the Autism Symptom SELF-Report (ASSERT; see Table 1)(Posserud, Breivik, Gillberg, & Lundervold, 2013) questionnaire for adolescents which is a brief (seven item), self-report measure of the level of autistic traits in adolescents. The trait anxiety levels of both groups were assessed using an abbreviated form (Fioravanti-Bastos, Cheniaux, & Landeira-Fernandez, 2011) of the State-Trait Anxiety Inventory (Spielberger, 1983a) (STAI; See Table 1). All participants and their parents gave informed consent prior to the study, according to the protocol approved by the local research ethics (patients: ClinicalTrials.gov Identifier: NCT02628808; controls: ethical approval number: 16-328).

Materials and design. The stimuli consisted of 10 pairs of identities (5 female), the same as previously used by Vilarem et al., (under review), which were originally drawn from the Radboud Face Database (Langner et al., 2010). These were modified using Adobe Photoshop CS5.1 (Adobe Systems, San Jose CA) and parametrically morphed using FantaMorph (Abrosoft <http://www.fantamorph.com/>) resulting in 10 pairs of identities * (4 morphs (emotion intensities) * 2 emotions (fear/anger) + four neutral

stimuli) * 2 orientation (the side of appearance of the emotional actor). The side on which each identity appeared was counterbalanced between participants, so that each actor was presented on the same side throughout the task for one participant but changed side between subjects. The two actors in each trial were always of the same gender. In total each participant completed 240 trials (80 neutral, 80, angry and 80 fearful), half of the original number of trials (Vilarem et al., under review), divided into 4 blocks of 60 trials in order to avoid tiredness and inattention effects. Stimuli were projected on a black background using Psychophysics-3 Toolbox (Brainard, 1997; Pelli, 1997) of Matlab (version R2014a) software (<http://uk.mathworks.com/>).

Task 1: Free action choice task.

In each trial participants initially faced with a grey screen for 1000 ms followed by a fixation cross, on which participants fixated throughout the trial. The cross appeared 500 ms before stimulus onset and remained on screen throughout the trial. After 500 ms, the target scene appeared until response or for a maximum of 1400 ms. Each target scene involved a waiting room with four chairs, the two central chairs were occupied by two individuals and the two chairs on the sides were free. In each trial, participants had to choose which of the two empty chairs they would like to sit in. Participants were informed that while there was no correct or wrong answer, there was correct movement for reaching the chair of their choice. This included pressing the left click on the mouse before starting the movement and holding it while moving the mouse cursor to the chair of their choice. If the click was released on the chair within 1400 ms this was considered a correct movement. Following a correct movement a grey check mark (non-social) appeared on the chair of the participant's choice, as feedback, to indicate a correct movement.

Task 2: Explicit categorisation of emotion.

Participants also completed a categorisation task after having been debriefed on the existence of emotional actors in the previous scenes. Participants were exposed to a more rapid presentation of the 160 emotional stimuli from the main task divided into two blocks of 80 trials each. In each trial participants saw a grey screen for 1000 ms followed by a central fixation cross for 500 ms before stimulus onset, similarly to the main task and then the target stimulus appeared for 600 ms. Participants were requested to fixate the cross throughout the trial and completed the task in peripheral vision. Following each stimulus, a slider appeared ranging from intense anger to intense fear via neutral. Participants were asked to use the mouse cursor after each scene to indicate which emotion appeared in the screen and its intensity. The side of the scale was counterbalanced between participants, so that half the participants used a scale with anger on the left side and fear on the right and vice versa.

Experimental procedure. Participants were seated at 40 cm distance from the laptop. They were told that they would see repetitions of a waiting room with four chairs, the central two of which are always occupied by two individuals. Before Task 1, participants were not informed about the emotional actors present in the scene but were told that the identities of the actors vary. They were being instructed to fixate the cross throughout each trial and to choose where they would like to sit using the mouse cursor. Before the four main blocks participants completed a training session consisting of 60 trials, with only neutral actors. During training, participants practiced the correct movement, while initially freely exploring the scene and subsequently fixating on the cross. Participants moved to the main task (4 blocks) only when 60% of correct movements was achieved in the training. When the task finished participants were asked questions to verify that they had not explicitly seen any emotions in the scene and were subsequently debriefed on the presence of the emotional actors. They then completed a one minute visual acuity test. Lastly, participants gave their answers to the anxiety and autistic traits scales verbally to the experimenter.

Sample size selection. We calculated the proportion of trials with correct responses with RTs > 200 ms and the proportion of invalid trials for each participant as a measure of exclusion. Invalid trials (Table 1) included ones with RTs < 200ms, non-response trials and missed (not reaching the chair) trials. Participants who were outliers in either of these two variables were excluded from the analysis. Two ASD participants and one TD participants were excluded from analyses resulting in a sample of 28 ASD and 33 TD participants. These 28 ASD participants were then automatically matched, using R Project for Statistical Computing (www.rproject.org) with 28 of the 33 TD participants according to chronological age, gender, full scale IQ (IQF), verbal IQ (IQV) and performance IQ (IQP) (see Table 1). The sample size was determined by an *a priori* power analysis given a predicted power = .80, an alpha level = .05 and a large effect size $\eta_p^2 = 0.14$. The projected sample size needed for this effect was approximately 27 participants in each group, thus a sample of 28 participants per group provides adequate power for our design (actual power = .83).

Anxiety levels. Given the high levels of comorbidity between anxiety and ASD (van Steensel, Bögels, & Perrin, 2011) and that anxiety increases sensitivity to social threat (Bishop, 2007) we compared the anxiety levels of the two groups and found no difference (see Table 1).

General data analysis. For Task 1, all non-response trials, incorrect-movement trials and trials with RTs inferior to 200 ms were excluded from all analyses. We performed a 2x2x4 repeated measures ANOVA on the proportion of choice and RTs with Emotion (anger vs. fear), Side (away vs. toward) and Intensity (4 levels) as within subjects' factors and Group (ASD vs. TD) as a between subject factor. The same analysis was performed within each group separately. From the remaining analyses any effects, interaction and comparisons that are not mentioned were not significant. Means and the standard

error of the mean (S.E.M) of all measures of interest, for each group in each condition are listed in Table 2.

For Task 2, due to time constraints, four TD and one ASD participants did not have the time to complete the emotion categorisation task. However, using extensive debrief questions we verified that they were not aware of the presence of emotional faces in the scene. Of the remaining subjects (ASD = 27, TD = 24), three participants (2 ASD and 1 TD) had low emotion categorisation accuracy (<50%). We performed the analyses both while including and excluding them and the results were comparable (see Supplementary Information), thus we included them in the final analyses. We analysed the overall accuracy for anger and fear recognition and their subjective ratings of the stimulus' emotional intensity (Table 3).

Insert Table 2 here

Matlab software and SPSS-18 were used for the ANOVA's and pairwise comparisons. The reported p-values are all two-tailed. Partial eta squared (η_p^2) is reported as the effect size of the F statistics, d of the parametric comparisons, and phi (ϕ) for the chi squared test comparing the distribution of gender across groups. A value of $\eta_p^2 = .01$ / d = .3/ $\phi = .1$ represents a small effect size, $\eta_p^2 = .06$ / d = .5/ $\phi = .3$ a medium one and over $\eta_p^2 = .14$ / d = .8/ $\phi = .5$ a large effect size(Cohen, 1988).

Insert Table 3 here

Bayes factor calculations. In order to investigate whether the ASD data supports a difference between Anger(Away-Toward) and Fear(Away-Toward) (H1), over and absence of a significant difference between the two (H0: null), we calculated the Bayes factor (Dienes, 2014) for each group. For this purpose we calculated the difference between the tendency to avoid and approach anger (=Anger(Away-Toward)) and the tendency to avoid and approach fear (=Fear(Away-Toward)) for each group. A Bayes factor uses prior knowledge or evidence in association with newly acquired data to describe the likelihood (llh) of the current data in supporting an alternative hypothesis (H1) against a null (H0) and is given by the formula $B = llh_{H1} / llh_{H0}$. If the Bayes factor is above 3 then the data provides support for the H1 while if it is less than 1/3 it provides support for the H0. If the Bayes factor is between 1/3 and 3 it means that our data is not sensitive enough to allow us to disentangle between the two hypotheses. We wanted to test the H1 that there is a significant difference between Anger(Away-Toward) and Fear(Away-Toward) in both the TD the ASD groups against an H0 that finds no difference between the two conditions. For this purpose, we used the difference between Anger(Away-Toward) and Fear(Away-Toward) of the neurotypical adult group (Vilarem et al., under review) as a prior for the calculation of the Bayes factor of the TD and ASD adolescents group. We then wanted to test the data for supporting the same H1 as compared to the null, this time in the ASD group

as compared to the TD adolescents group and we used the difference between the two conditions of the TD adolescent group as the prior for the calculation of the Bayes factor of the ASD group. This process allowed us to firstly verify whether the data supports a difference between the two conditions in the two adolescent groups in the same way as it has been previously demonstrated in adults (replication) and secondly to test whether the data of the ASD group supports the same difference given the TD adolescent data as a prior.

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Author contributions

C.I., E.V., C.C. and J.G. designed the study. CI conducted the experiment and performed the data analysis. C.I., C.C. and J.G. prepared the manuscript. A.L., F.A. and R.D. conducted the patients' clinical evaluations. All authors reviewed and approved the final manuscript.

Figures and legends

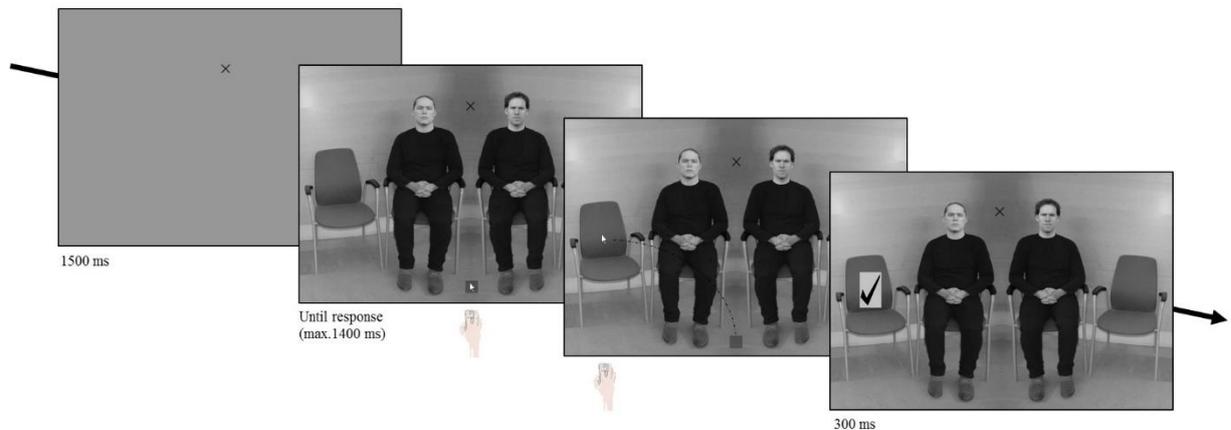


Figure 1. Time course of a trial of the free action task. Initially participants saw a grey screen for 1500 ms including a cross at the top of the screen. Subsequently, they were faces with a scene stimulus representing a waiting room and they had a 1400 ms window to direct the mouse cursor to the seat of their choice. Following completion of their action, a grey check mark (non-social) appeared on the chosen seat for 300 ms to indicate that the movement was correct. Importantly throughout the trial participants fixated the cross at the top of the scene.

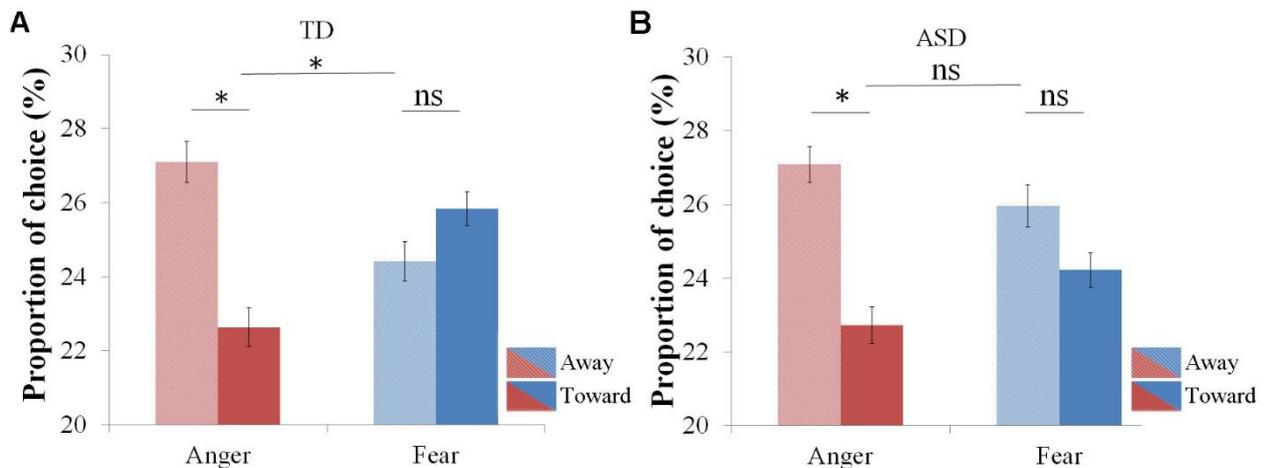


Figure 2. Emotion-by-Side interaction on the proportion of choice for the A) TD and B) ASD groups. Within subjects error bars represent Mean \pm S.E.M.; * $p \leq 0.05$; ns $p > 0.05$.

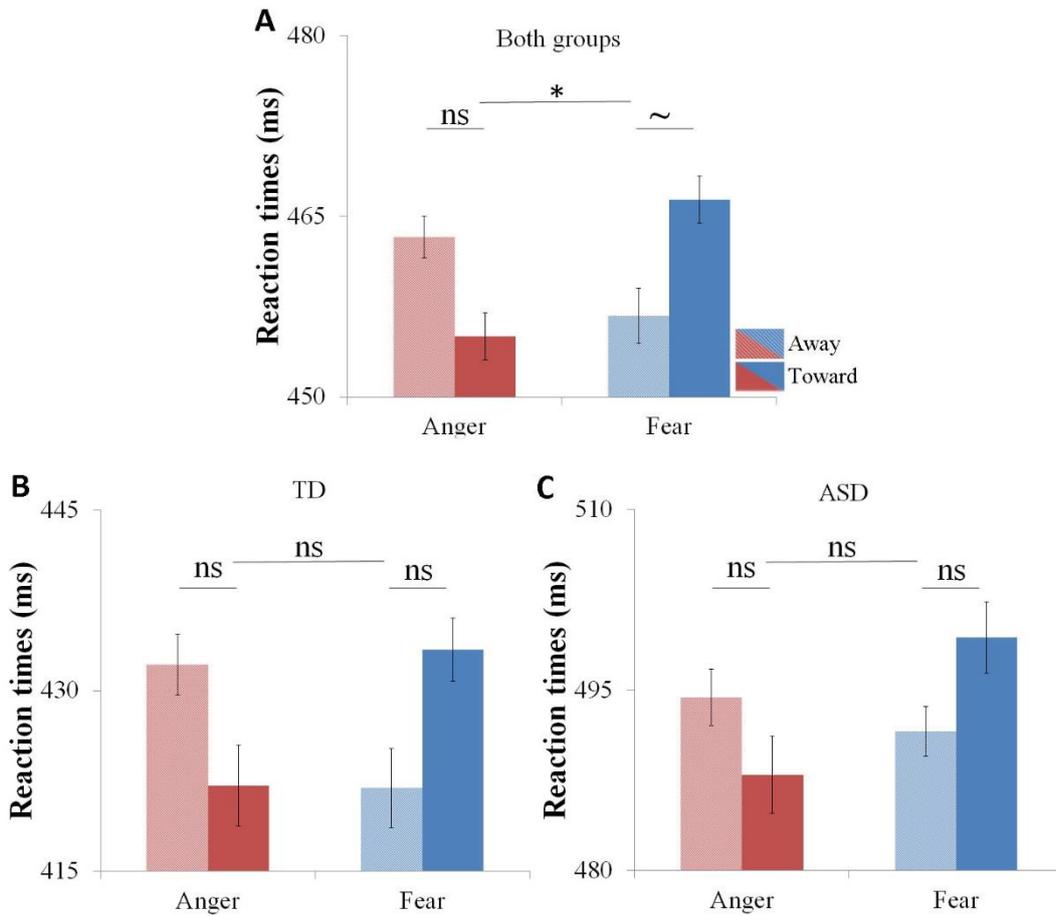


Figure 3. A) Emotion-by-Side interaction on all participants' RTs, B) on the TD group's RTs and C) on the ASD group's RTs. Note that the within group interactions were no significant and that the RTs range in the within group graphs is different because of a significant effect of group on RTs. Within subject error bars represent Mean \pm S.E.M.; * $p \leq 0.05$; $\sim p = 0.08$, ns $p > 0.1$.

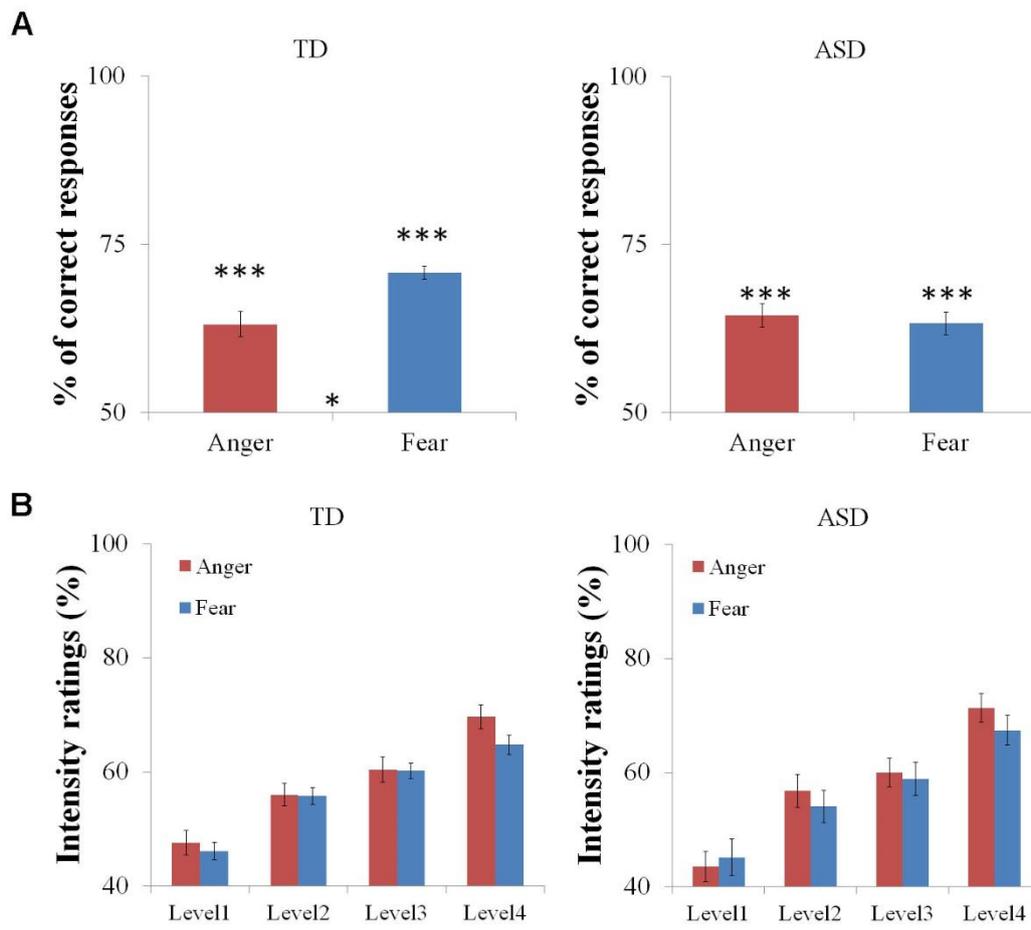


Figure 4. Explicit emotion categorisation results. A) Emotion recognition accuracy for each emotion for each group. Note that in the TD group there was an effect of emotion, with overall higher accuracy for the emotion of fear. B) Emotion-by-Intensity interaction for each group. Within subjects error bars represent Mean \pm S.E.M.; *** $p \leq 0.001$; * $p \leq 0.05$.

Tables

Table 1. Mean (S.E.M.) of chronological age, gender, IQF, IQV, IQP, ASSERT, trait anxiety, total invalid trials for both groups and SRS, ADOS total, ADOS sub scores and ADI scores for the ASD group.

	ASD (n=28)	TD (n = 28)	Test value, p value, effect size value
Age	12.3 (0.28)	13.6 (0.21)	t(54) = -0.807, p = .423, d = .22
Gender	Males n=24	Males n=22	$\chi^2(1) = 0.487, p = .485, \phi = .093$
IQF	102.4 (3.4)	101.9 (2.5)	t(54) = 0.051, p = .959, d = .013
IQV	109.2 (4.4)	102.1 (2.4)	t(54) = 1.415, p = .164, d = .38
IQP	99.2 (3.8)	99.3 (2.7)	t(54) = -0.015, p = .988, d = .005
Anxiety (STAI)	13.9 (0.7)	14 (0.7)	t(54) = -0.183, p = .855, d = .05
Invalid trials	42(4.5)	47(4.1)	t(54) = -0.872, p = .387, d = .23
Autistic traits (ASSERT)	5.4 (0.5)	3.5 (0.5)	t(54) = 2.620, p = .011, d = 1.004
SRS total	103 (2.5)	NA	NA
ADOS	12.3 (0.48)	NA	NA
ADOS_{com}	3.9 (0.2)	NA	NA
ADOS_{RSI}	8.4 (0.34)	NA	NA
ADOS_{imag}	0.7 (0.09)	NA	NA
ADOS_{ster}	1.2 (0.15)	NA	NA
ADI social reciprocity	17 (0.6)	NA	NA
ADI communication	13 (0.6)	NA	NA
ADI restricted	5.5 (0.3)	NA	NA

Table 2. Mean (S.E.M.) proportion of choice and RTs per group per condition.

	Conditions	Anger-Away	Anger-Toward	Fear-Away	Fear-Toward	Mean
ASD	Proportion (%)	27.1 (0.49)	22.7 (0.57)	26 (0.49)	24.2 (0.44)	25
	RTs (ms)	494 (9)	488 (19)	492 (9.5)	499 (9.8)	493
TD	Proportion (%)	27.1 (0.56)	22.64 (0.53)	24.42 (0.53)	25.84 (0.46)	25
	RTs (ms)	432 (10)	422 (11)	422(9.9)	433 (9.2)	427

Table 3. Mean (S.E.M.) of emotional intensity ratings per group.

	Conditions	Level 1	Level 2	Level 3	Level 4
ASD N=27	Intensity (%) of anger	44 (2.5)	57 (2.8)	60 (2.4)	71 (2.4)
	Intensity (%) of fear	45 (3.1)	54 (2.7)	59 (2.7)	67 (2.5)
TD N=24	Intensity (%) of anger	48 (1.7)	56 (1.9)	60 (2.1)	70 (1.7)
	Intensity (%) of fear	46 (1.9)	56 (1.5)	60 (1.7)	65 (1.5)

Chapter 3 conclusion

In chapter 3, I presented the limited available literature which proposes that individuals with ASD might be characterised by difficulties in the regulation of responses during social interactions, independently of their ability to decode emotional signals. I, then, presented the second experiment of this Ph.D. which investigated the effect of task-irrelevant social threats on the regulation of behavioural responses in adolescents with and without ASD. This took place in an ecological, interactive context, where the social threats were implicit (motivating condition).

The main messages of experiment 2 are the following: although TD adolescents were quicker and more influenced by intensity than ASD adolescents, both groups 1) demonstrated preserved ability to discriminate social threats in visual periphery, 2) showed a tendency to avoid the emotional agents in general, 3) preferred to avoid anger as compared to approaching it and 4) did not show a preference between approaching and avoiding fear, although their responses when they approached fear were significantly delayed as compared to avoiding it.

When emotion decoding abilities are preserved, adolescents with ASD are able to use task-irrelevant threat in order to adapt their behaviours in the same way as TD adolescents. Neither group showed a preference to approach or avoid fear although both groups were characterised by delayed RTs when approaching fear, suggesting that in adolescents this tendency might not be prioritised.

Chapter 4: General Discussion

4.1 Summary of goals

In this Ph.D. two experimental studies were conducted and aimed at characterising the perception of social threats in adolescents with ASD. Study 1 investigated the processing of facial displays of threat by looking at the mechanism behind the integration of task-irrelevant gaze direction with facial expressions of anger and fear. In study 2 we moved a step further and addressed the responses of adolescents with ASD to task-irrelevant facial displays of threat.

4.2 Preserved processing of social threats in adolescents with autism spectrum disorders

A large number of studies has investigated deficits in emotion perception in individuals with ASD, including children, adolescent and adult participants. The most dominant view holds that individuals with ASD are characterised by deficits in emotion processing. However, approximately one in four studies investigating emotion perception in ASD fails to reveal atypicalities in the processing of facial affect in ASD as compared to neurotypical controls (Gaigg, 2012; Harms et al., 2010), rendering the evidence for an overall emotion processing deficit in ASD inconsistent. The performance of the ASD group depends strongly on several methodological factors, including the implementation or not of a fixation point at the stimulus' eye-level, the type of control group used, the variables on which the groups are matched and the type of stimuli used; whether these are rapid, realistic or not and of variable intensity.

In section 2.3 (Ioannou et al., 2017), we investigated the decoding of facial expressions of anger and fear while controlling for as many methodological factors as possible. The task was a 2AFC emotion categorisation task, the stimuli included facial displays of anger and fear of variable intensity and the presentation of the stimuli was rapid to tap into the reflexive stage of processing. We chose a control group of TD adolescents, who had the same full, verbal and performance IQ to eliminate potential effects on the results. Moreover, our two groups had comparable levels of anxiety excluding one more difference that might have influenced the results given that anxiety is comorbid with ASD (van Steensel et al., 2011) and impacts on one's sensitivity to social threat by enhancing it (Bishop, 2007). Critically, we implemented a pre-stimulus fixation jitter to implicitly guide participants' attention to the stimulus' eye-region in the start of each trial. Under these well controlled conditions we found that while TD adolescents were overall better in emotion decoding than the ASD group, gaze direction impacted on the processing of threat similarly in the ASD and TD groups by enhancing the perceptual sensitivity to salient combinations of threat. The impact of gaze direction on the processing of social threats in TD

and ASD adolescents is the same in neurotypical adults too (El Zein et al., 2015). These results suggest that the mechanism behind the processing of threatening emotions in ASD is intact, at least in the case of anger and fear. Adolescents with ASD can accurately process social threats and gaze direction impacts on this processing by determining the saliency of the threat to the observer and by enhancing their sensitivity to the most salient ones.

Furthermore, following the main task (free action task) in experiment 2, participants completed an explicit emotion categorisation task in visual periphery, where threat expressions of varying intensity were categorised as expressing anger or fear. Similarly to the first experiment strict methodological factors were taken into account; well matched groups on verbal, performance and full IQ, same levels of anxiety and larger sample size. There were two critical differences: the emotions were presented in visual periphery while participants fixated at a central fixation cross and participants were asked not only to categorise the emotions but also, while doing so, to indicate the intensity of the expressed emotion. Our findings provide a replication of the results of study 1, in that both groups showed emotion categorisation of both anger and fear above chance and their subjective ratings of the expressions' intensity increased as the actual, objective intensity of the stimuli itself increased. Thus, we can argue that the processing of social threats in ASD is preserved both in direct view and in visual periphery.

4.3 Preserved responses to social threats in adolescents with autism spectrum disorders

Having demonstrated accurate processing of social threats and comparable influence of gaze direction on this processing in ASD and TD adolescents, the question remained whether adolescents with ASD understand the communicative value of those social threats in order to prepare adaptive responses to them.

The literature investigating the responses of individuals with ASD to other people's emotional signals is limited. To our knowledge only 10 studies have addressed this question (Bacon et al., 1998; Blair, 1999; Celani et al., 1999; Corona et al., 1998; Dissanayake et al., 1996; Hobson et al., 2009; Klapwijk et al., 2017; Loveland & Tunali, 1991; Sigman et al., 1992; Yirmiya et al., 1992). To do so they focused on video recorded responses of ASD children during social situations where the participants' parent or one of the experimenters would show strong fear, discomfort or distress in response to something unfortunate that happened to them during the interaction. This could include losing their wallet (Loveland & Tunali, 1991) or accidentally hurting themselves (Bacon et al., 1998; Corona et al., 1998). In other cases, the parent or the experimenter would perform facial expressions in response to objects in the surrounding environment, such as fearful reactions to toy robots that move in the

environment (Sigman et al., 1992). More recently, relatively more refined tasks have been implemented such as ones using anticipatory concern as a means for evaluating responses to a third person's expected distress (Hobson et al., 2009) or using adapted versions of the dictator game with the interlocutor's emotional expressions acting as feedback for past unfair decisions (Klapwijk et al., 2017). The results across them are quite robust. They point to comparable basic responses between TD and ASD individuals, i.e. responses to anger which signals direct threat as a result of violations of social expectations (Averill, 1982), but differential affiliative responses, i.e. to happiness, or empathic responses, i.e. to others' distress. Overall, ASD participants were more likely to play with their toys instead of orienting to the experimenter after they had demonstrated distress, fear or pain while TD children usually would respond to the adult with concern, suggesting that ASD individuals do not learn about the aversive and/or hedonistic value of emotions.

While those findings are important to provide the basis for investigating responses of individuals with ASD to others' emotional states, they do not directly assess the action tendencies that are evoked by them. In other words, such paradigms place high level social demands on the individuals given that they require an inhibition of the participants' current activity, their orientation towards the experimenter and an expression of *overt* concern towards them, rather than a direct response to the emotional stimulus/agent. Such results cannot prove an inability of individuals with ASD to respond to others' affect, especially because participants in some of those studies were somehow aware of the emotional display in question and had registered to some level the event in question, given some physiological arousal in response to distress (Blair, 1999). Similarly to experiment 1, in experiment 2, we ensured the basic methodological requirements (section 1.3) relevant for this study; groups matched on full, verbal, and performance IQ, gender and age and a fixation cross in the relevant for this study location in the scene. Critically, we employed a paradigm (Vilarem et al., under review) which creates an everyday realistic scenario without explicit social demands where active responding (performing an action) is an inseparable and essential part of the paradigm rather than an additive demand. Moreover, the paradigm assesses responses to two negative evolutionary emotions which are known to induce opposite action tendencies in the observer (Vilarem et al., under review) and which have been parametrically manipulated to express four intensities, thus being more ecologically valid. Using this task we were able to demonstrate comparable behaviour between ASD and TD adolescents in response to both anger and fear. Although the TD group was quicker than the ASD group and the speed of their responses was influenced by intensity, both groups showed a clear preference to avoid the emotional actor in general and particularly when the emotional actor expressed anger. In the case of fear, both groups chose to equally approach and avoid it, while not demonstrating a clear preference. The above findings are the same with a group of neurotypical adults that have been previously tested with the

same paradigm (Vilarem et al, under review). While neurotypical adults showed no behavioural preference in response to fear, they had shown a speed advantage (increased velocity) when they approached it as compared to avoiding it suggesting that in this task fear is an emotion inducing approach tendencies in the observers. In our adolescent groups this was not the case, as we had no results in the temporal dynamics of the movement kinematics (see Appendix 2). Contrary to adult results we found that both ASD and TD adolescents took longer time to approach fear as compare to avoiding it, potentially reflecting the overall preference of both adolescent groups to avoid the emotion in the scene. Given that their emotion decoding abilities were comparable these findings indicate that individuals with ASD are able to decode and use social threats in order to adapt their behaviour in the same way as TD adolescents.

4.4 Impaired social motivation and/or impaired mechanisms?

The most dominant view in terms of emotion processing abilities in ASD holds that these individuals are unable to process emotion. In this thesis, I presented findings of comparable decoding and processing of facial expressions of social threats in adolescents with and without ASD. Our results stem not only from a 2AFC task, where attention was directed to the eye-region of the stimulus and participants had to categorise the faces as fearful or angry, but also from participants' emotion categorisation performance in visual periphery in a task where both the emotion and its intensity were categorised. Importantly, in the second experiment, we were able to assess whether adolescents with ASD are sensitive to different levels of emotion strength because previous studies find that they are impaired at low intensities (Law Smith et al., 2010). In our study subjective emotion ratings increased as the actual emotional intensity itself increased. Independently of an overall reduced emotion recognition accuracy in ASD, we can argue that individuals with ASD are able to decode facial expressions of anger and fear both in direct view and in visual periphery and they can discriminate between different levels of emotion strength. Moreover, they can take into account contextual gaze cues when processing social threats and the influence of those cues is the same in adolescent with and without ASD as in neurotypical adults.

In a third experiment (see Appendix 4: Safra et al., in preparation) we recently demonstrated that adolescents with ASD are able to accurately process cues of dominance and trustworthiness and to combine them in order to make likability evaluations (Todorov, Said, Engell, & Oosterhof, 2008). In this study both abilities were intact but adolescents with ASD were less sensitive to dominance cues and they granted less weight to them during likability evaluations. Our results are in line with such findings, in that they provide evidence for preserved abilities to detect and combine cues in ASD (Caulfield, Ewing, Bank, & Rhodes, 2016; Caulfield, Ewing, Burton, Avard, & Rhodes, 2014; Ioannou et al., 2017; Philip et al., 2010; White, Hill, Winston, & Frith, 2006) and suggest that socio-emotional and

communicative deficits in this group might exist independently of their ability to process others' emotional signals. Two alternative frameworks attempt to characterise the impaired behavioural performance of individuals with ASD in decoding facial affect; the behavioural self-regulation account (Bachevalier & Loveland, 2006; Hellendoorn, 2014; Loveland, 2005; Loveland, 2001) and the social motivation account (Chevallier, Kohls, et al., 2012; Dawson et al., 2005).

The behavioural self-regulation account suggests that individuals with ASD are characterised by deficits in the mechanism behind the processing of emotional signals and/or the regulation of adaptive responses to those signals. Throughout this thesis we have shown that although the TD group was overall more accurate in categorising social threats and quicker in selecting the adequate course of action in response to these threats, adolescents with ASD did not differ from their TD peers in either the processing of social threats, the impact of gaze direction on this processing or the use of social threats for behavioural adaptation. Both groups recognised anger and fear accurately well above chance in both direct view and in visual periphery, they were able to integrate gaze direction while processing social threats and the influence of gaze direction on the processing of social threats was the same across groups; gaze direction enhanced the participants' sensitivity to the most salient combinations of threat. Additionally, both groups used implicit social threats in order to adapt their behaviour and avoid the threatening stimulus. This was particularly evident in the case of anger, a signal of direct threat to the observer. In the case of fear, we did not observe a behavioural difference in the tendency to approach or avoid it, but when participants approached it their reaction times were longer suggesting that this preference in both groups is not prioritised, potentially because adolescents are characterised by enhanced reactivity to threat (Hare et al., 2008). Although we cannot conclude about the responses of adolescents with ASD to approach oriented emotions, we can argue that a deficit in the mechanism behind the preparation of adaptive responses to emotional signals cannot be deficient in ASD, as this group demonstrates avoidance behaviour similar to TD matched controls in response to social threats.

On the contrary our findings are in line with social motivation accounts (Chevallier, Kohls, et al., 2012; Dawson et al., 2005; Grelotti et al., 2002) which propose that individuals with ASD are not characterised by impaired mechanisms behind the targeted social abilities or by social cognition failures, but by deficits in the motivation and reward system. According to this theory, social information is granted less weight and social engagement is not spontaneous. For instance, social motivation decreases the weight that is ascribed to invariant facial cues, i.e. trustworthiness features, when participants are asked to make likability judgments, although these participants demonstrate preserved processing and integration of these cues with dominance ones (see Appendix 4: Safra et al., in preparation). Growing evidence demonstrates that within the social world (Chevallier et al., 2013) or

when ASD individuals have been motivated to attend to it (Begeer et al., 2006; Ioannou et al., 2017; Senju et al., 2009), group differences disappear and individuals with ASD perform like controls. Taken together, our results fit social motivation accounts in that although ASD individuals demonstrated overall reduced emotion decoding accuracy as compared to TD adolescents (3% difference), both groups processed emotions accurately and integrated gaze direction in a way congruent with the saliency of the expressed threat.

Using a paradigm that provides action possibilities in response to implicit threats (no social response demands) we demonstrated comparable responses to social threats in TD and ASD adolescents (section 3.1). According to the social motivation framework and past evidence for intact responses to anger, some physiological responses but impaired affiliative responses to another's distress (Bacon et al., 1998; Blair, 2003; Hobson et al., 2009; Klapwijk et al., 2017; Loveland & Tunali, 1991) we expected that individuals with ASD will use anger to adapt their behaviour given that reactions to this emotion are fundamental for survival. However, we expected that they will either not approach fear or they will show no preference to avoid or approach it given that in this task the emotion is clearly social and affiliative. To our surprise none of the groups showed a preference in the case of fear, where participants avoided it and approached it equally. Moreover, both groups showed a speed advantage when avoiding fear suggesting that this choice was preferred and reflecting their overall tendency to avoid the emotional actors. Thus, with the present data we cannot draw conclusions in terms of their ability to respond adaptively to social, affiliative emotions. As stated by Gibson, (1979), social affordances, which are the ones provided by other people, are equally direct as the ones in the physical world and depend equally much on the collection of information from the social environment. If individuals with ASD are characterised by diminished spontaneous social engagement (social orienting, seeking and maintaining) and consequently atypical orientation to and spontaneous perception of information from the social world, it could be argued that their responses to emotional signals requiring social engagement are different –not impaired- than that observed in TD controls. In a dictator game, ASD behaved unfairly in response to others' angry expressions, but TD adolescents behaved unfairly in response to both angry and happy expressions of others. Importantly these expressions were others' reactions to the participant's previous (1 week before) unfair decisions. Although ASD individuals behaved unfairly in response to anger, the TD group did so also in response to happiness, which is expected to indicate content over a previous unfair offer (Cacioppo & Gardner, 1999; Klapwijk et al., 2016; Kleef, Dreu, & Manstead, 2010).

Although the present data does not allow us to draw such conclusions, two possibilities arise: 1) individuals with ASD fail overall to understand the affective meaning of clearly social and affiliative emotions, or 2) they understand the meaning of those emotions but use different heuristics, such that,

for instance, they treat them similarly to negative ones. In order to disentangle that, future studies should tackle the responses of individuals with ASD to emotions that are clearly social, such as happiness, which is an affiliative and approach oriented emotion (Hess, Adams, & Kleck, 2005; Soussignan et al., 2012). A preliminary study could use an adapted version of the free action task (section 3.1) using only neutral and happy facial expressions, where approach tendencies would be induced only by the happy individual. Although happiness is an emotion that can be used in this context, the present task might not be ideal. Happiness is an appetitive emotion that taps to a different neural system than threat (Bayliss, Frischen, Fenske, & Tipper, 2007; Cacioppo & Gardner, 1999) and engages reward processing (Monk et al., 2008) which makes it adaptive in terms of establishing and maintaining social interactions. Similarly to our rationale in experiment 2, it would be best to choose a refined task which uses happy facial expressions during social interactions and which is proven to influence the responses of neurotypical individuals. One of the most robust findings in the literature points to inflated likability ratings for objects of neutral valence, following observation of an avatar that stares at them and smiles (Bayliss et al., 2007; Bayliss, Griffiths, & Tipper, 2009; Soussignan, Schaal, Boulanger, Garcia, & Jiang, 2015). Importantly, in those tasks negative and neutral emotions do not produce the opposite effects of happy ones but rather no effects. Hence, those tasks are ideal candidates for investigating the comprehension of the communicative value of positive, affiliative emotions in ASD and the processing of reward contingencies provided by that emotion.

4.5 Social threats: anger and fear

Across both studies of this Ph.D. we evaluated the perception of social threats and specifically of facial displays of anger and fear in adolescents with and without ASD. As early as Darwin, (1872) facial expressions of anger and fear are considered aversive stimuli, evolved to signal threat to the observer and to serve survival-relevant functions, such as the initiation and regulation of adaptive responses to the present threat. As a result they serve ideal cases of emotions for assessing both parts of the action-perception link in the context of emotion processing in ASD, as they enable us to investigate both how those individuals process emotion and how they use it to adapt their behaviour. Importantly, the recognition of anger and fear relies on diagnostic information from the eyes (Schyns, Gosselin, & Smith, 2009), particularly if the facial expressions of these emotions are morphed (Wegrzyn, Bruckhaus, & Kissler, 2015). Information from the eye-region is critical for the decoding of anger and fear and attention to this region is diminished in ASD (see section 1.3.4). Thus, anger and fear are ideal candidate emotions for disentangling between a processing deficit in ASD and an impaired behavioural performance resulting from diminished attention to the eye-region, which was the aim of the first experiment.

Independently of their similarities, those emotions differ on several other aspects. An angry expression is interpreted as signalling a direct threat to the observer while fear constitutes a more complicated case (Marsh, Ambady, & Kleck, 2005). Firstly, fear is widely accepted as a stimuli that signals a danger in the environment surrounding the observer rather than directly against them (Whalen et al., 2001). There is evidence that when compared to angry or neutral facial expressions, fear implicitly enhances the observer's ability to detect peripheral targets, thus enhancing environmental monitoring (Taylor & Whalen, 2014). Hence, anger and fear are both threatening emotions, which however, signal different sources of threat. A lot of studies have by now provided evidence for a strong contextual influence of gaze direction on the processing of social threats in neurotypical populations, which is congruent with the above distinction between the sources of threat signalled by each emotion (refer to section 2.1). When anger is paired with direct gaze it is better and quicker recognised because it signals that the observer is under imminent threat, while fear is better and quicker recognised when paired with averted gaze because it signals a threat in the surrounding environment. Gaze direction leads to an enhancement of the observer's perceptual sensitivity to these salient combinations of threat, in the same direction as it had been previously expected. In section 2.3 (Ioannou et al., 2017) we showed that this is also the case in adolescents with ASD.

Secondly, although both anger and fear had been thought to induce avoidance tendencies in the observer, anger does facilitate avoidance behaviours and is clearly threatening, while fear has been found to elicit behavioural approach (Hammer, & Marsh, 2015; Marsh et al., 2005). Using an implicit association test (IAT) combined with an approach-avoidance lever task, Hammer et al., (2015) investigated whether this is the result of the resemblance of fearful faces to infantile ones. Participants used the approach-avoidance lever to respond to fearful and angry facial expressions as well as to neutral infant and adult faces, in congruent and incongruent blocks. In the congruent ones fearful and infant faces as well as angry and adult faces were categorised by the same lever movement, whether push or pull. In the incongruent block the opposite was the case. Participants were quicker at responding when infant and fearful faces were paired together as compared to infant faces being paired with angry ones or fearful faces being paired with adult ones. Importantly, participants pulled the lever towards them when fearful stimuli appeared. Thus, while anger elicits avoidance due to signalling threat, fear can induce approach tendencies. This was not the case in our second study although the TD group indicated a tendency to approach fear more than anger but both groups were found to similarly move towards and away from fear, not indicating a clear preference.

Given the above and the advantage of fear in signalling enhanced threat when it is directed towards the environment, we could speculate that the action tendencies that are evoked by fearful faces might depend on the context. For example, in the studies mentioned above and in experiment 2

(section 3.1) the fearful expressions used were directed towards the observer. Maybe contextual effects are more relevant in the perception of threat from a fearful face because they signify the direction of threat. Recently, a study investigated the anger superiority hypothesis in typical adults, which refers to a speed advantage in detecting anger when this is embedded in crowds of neutral faces (Taylor & Barton, 2015), as compared to the detection speed of other threatening faces in neutral crowds. Participants saw small and big crowds of individuals who looked either straight at the participant or at one of the two sides. In each trial all faces had a neutral expression except one individual who either expressed anger or fear. In line with the authors' hypothesis anger was detected quicker when it was directed towards the observer than when it was averted. This was most evident in smaller crowds. Critically, contrary to the authors' expectations, fearful expressions were detected quicker than angry ones and this was independent of the direction of the face or the size of the crowd. This could offer a potential explanation for an absence of a behavioural preference between approaching and avoiding fear, which was evident not only in our experiment (section 3.1) but also in the original one in neurotypical adults participants (Vilarem et al., under review). We could argue that while anger signals a direct threat to the observer, fearful expressions are perceived as instinctive reactions to threat, the source of which is highly ambiguous. Therefore fear is suggested to be more salient irrespective of where it is directed (Taylor & Barton, 2015) and the absence of a behavioural preference to approach or avoid fear could result from such an ambiguity from the source of threat, at least during adolescence, a period characterised by enhanced reactivity to threats in comparison to children and adults (Hare et al., 2008). Indeed, both ASD and TD adolescents showed a speed advantage when avoiding fear as compared to approaching it.

4.6 Limitations

Our studies investigated emotion abilities specifically in adolescents with ASD and we cannot draw conclusions about whether the same effects are found in children and adults, although in terms of processing and combining of socio-emotional signals, preliminary evidence suggests that adults with ASD can integrate anger with body postures in order to process social threat (Brewer et al., 2017). Future studies should tackle the processing of and responding to social threats in those age groups, with paradigms that take into consideration all the necessary methodological requirements and constraints and are adapted for each developmental age (see section 1.3). Moreover, our samples were predominantly male, which limits our ability to investigate gender differences in threat perception. ASD is considered a predominantly male condition, with 1 in 10 diagnosed individuals being female by the early 2000s and 1 in 4 diagnosed individuals being female lately (Baron-Cohen, 2002; Fombonne, 2009; Hall et al., 2012). Recently, evidence points to under-diagnosis of ASD in female individuals probably because they exhibit a greater drive for affiliation (Brody & Hall, 2008; Neufeld, Ioannou, Korb,

Schilbach, & Chakrabarti, 2016), enhanced social sensitivity and less socio-communicative difficulties than males (Connellan, Baron-Cohen, Wheelwright, Batki, & Ahluwalia, 2000; McClure, 2000), abilities which are found to be preserved in females with ASD (Lai et al., 2011). Future work should attempt to disentangle whether such differences raise differential threat processing between the two ASD gender groups.

In the present experiments, we were interested in the perception of social threats, that is anger and fear, which is a very narrow set of emotions and does not allow for generalisation of these effects across other emotions. The literature regarding emotion perception in ASD is inconsistent and points to behavioural deficits primarily in the perception of negative emotions (Harms et al., 2010). Our findings reveal intact processing of two negative emotions, anger and fear. Future studies should target larger sets of emotions. Moreover, although we recorded some physiological data, and specifically eye-tracking, we were not able to use it (see Appendix 3). Follow-up studies should use a larger range of techniques with better eye-tracking systems, which are stable rather than mobile. Lastly, due to resource limitations we were not able to use imaging techniques on adolescents and future work should target the neural mechanisms behind the processing of and the responses to social threats in adolescents with and without ASD.

Conclusion

This doctoral thesis investigated the processing of and response to social threats that is facial expressions of anger and fear, in adolescents with and without autism. I argued that while the literature is inconsistent in terms of the emotion processing abilities of individuals with autism, it is important to revisit methodological factors that might bring this group to a disadvantage and lead to their impaired behavioural performance. Specifically, individuals with autism are characterised by diminished attention to social cues, such as the eye-region, which gives rise to the possibility that rather than a generalised deficit in the mechanism behind emotion processing, an inattention to the relevant aspects of the social world could underline observed behavioural deficits. To disentangle between the two I focused on two recent theoretical frameworks in the context of social threat perception: a) the behavioural self-regulation account which proposes that deficits exist at the mechanism behind either/both the processing of threat or the regulation of adaptive responses to this threat; b) the social motivation account which presupposes that both of those mechanisms are intact and behavioural deficits result from a lack of spontaneous orientation to the social world and engagement with it.

Taking several methodological factors into account we have shown that both adolescent groups can accurately process facial displays of threat both in direct view and in visual periphery and they can discriminate between different levels of emotion strength. Regardless of individuals with autism being overall less accurate than typically developing ones, in both groups gaze direction acts as a contextual factor that impacts on the processing of social threats by enhancing the perceptual sensitivity to salient combinations of threat. The mechanism behind this influence is the same in both adolescent groups and the same with a previously tested adult group. Similarly, both groups showed a tendency to avoid angry individuals rather than approaching them, but neither group showed a clear behavioural preference in the case of fear, which is in need of further investigation. Although typical adolescents were quicker at responding to social threats than adolescents with autism and this was influenced by intensity, both groups exhibited larger reaction times when they approached fear and shorter when they avoided it, stressing the overall avoidance of threatening agents in adolescence which is a period characterised by increased reactivity to threat.

To conclude, our results point to intact mechanisms behind the processing of social threats and specifically anger and fear with both groups demonstrating accurate processing well above chance, although further investigation is needed to confirm whether the groups are actually comparable given a 3% difference between them. The results more confidently point to intact mechanisms behind the integration of social threats with gaze direction and the preparation of avoidance responses to anger in autism, contradicting self-regulation accounts and providing preliminary support for the social

motivation theory. However, those results should be regarded carefully given that we did not investigate the direct impact of social motivation on those abilities and future studies need to research this further. Our findings do not allow for conclusions in terms of the processing of and responding to affiliative emotions in ASD, which is essential for drawing further conclusions regarding a social motivation deficit in autism. I provide methodological details of how this could be tackled by future studies.

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Appendices

Appendix 1: Supplementary Information (Experiment 2)

Supplementary Information for

Adolescents with autism can use implicit social threat to adapt their behaviour

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Supplementary Data

Proportion of choice analyses while co-varying out ASSERT. Between Group analyses: We repeated the analysis while co-varying out participants' autistic traits score, as measured by the ASSERT (see Method in main text for details). We found comparable results and no interactions with ASSERT: Effect of side: $F(1,53) = 5.927$, $p = .018$, $\eta_p^2 = .101$; Side*Intensity: $F(3,159) = 3.067$, $p = .03$, $\eta_p^2 = .055$; Emotion*Side: $F(1,53) = 6.243$, $p = .016$, $\eta_p^2 = .105$; Emotion*Side*Group: $F(1,53) = 0.796$, $p = .376$, $\eta_p^2 = .015$; Emotion*Side*Intensity: $F(3,159) = 4.245$, $p = .006$, $\eta_p^2 = .074$; Emotion*Side*Intensity*Group: $F(3,159) = 0.717$, $p = .543$, $\eta_p^2 = .013$. When we did not co-vary ASSERT there was a trend for a Side*Intensity*Group interaction ($p = .086$), see Results in main text) which was not found to be insignificant when we co-varied ASSERT ($F(3,159) = 1.156$, $p = .328$, $\eta_p^2 = .021$). However, within group analyses (below) yielded exactly the same results as in the main text and the interaction between intensity and side differed between groups and was significant only in the TD group.

Within group analyses: We repeated the analysis within each group while co-varying out the ASSERT score. The results were the same with the Results in the main text and ASSERT did not interact with other variables (ASD: Effect of side: $F(1,26) = 3.939$, $p = .058$, $\eta_p^2 = .132$; Side*Intensity: $F(3,78) = 2.223$, $p = .092$, $\eta_p^2 = .079$; Emotion*Side: $F(1,26) = 2.035$, $p = .166$, $\eta_p^2 = .073$; Emotion*Side*Intensity: $F(3,78) = 1.227$, $p = .305$, $\eta_p^2 = .045$; TD: Effect of side: $F(1,26) = 1.969$, $p = .172$, $\eta_p^2 = .07$; Side*Intensity: $F(3,78) = 3.066$, $p = .033$, $\eta_p^2 = .105$; Emotion*Side: $F(1,26) = 4.145$, $p = .052$, $\eta_p^2 = .137$; Emotion*Side*Intensity: $F(3,78) = 4.054$, $p = .01$, $\eta_p^2 = .135$) and no other interactions or effects were significant.

Reaction times analyses while covarying out ASSERT. Between Group analyses: We repeated the analysis while co-varying out participants' ASSERT score. We found comparable results: Effect of group: $F(1,53) = 5.761$, $p = .02$, $\eta_p^2 = .098$; Emotion*Side: $F(1,53) = 4.752$, $p = .034$, $\eta_p^2 = .082$; Emotion*Side*Group: $F(1,53) = 0.224$, $p = .638$, $\eta_p^2 = .004$. We did find a trend for an interaction between emotion, side, intensity and ASSERT ($F(3,159) = 2.679$, $p = .056$ Greenhouse-Geisser corrected, $\eta_p^2 = .048$) but this was not significant in either group as within group analyses (below) revealed.

Within group analyses: Within group analyses of participants' RTs while co-varying out ASSERT revealed exactly the same results as in the main text section. Except of an effect of intensity in the TD group ($F(3,78) = 3.183$, $p = .028$, $\eta_p^2 = .109$) there were no other significant effects or interactions ($p \geq 0.104$) in either group. The interaction between emotion, side, intensity and ASSERT was not significant in either group (ASD: ($F(3,78) = 1.378$, $p = .256$, $\eta_p^2 = .05$; TD: ($F(3,78) = 2.071$, $p = .111$, $\eta_p^2 = .074$).

Post-test emotion categorisation accuracy results excluding 3 participants who were outliers. In the emotion categorisation post-test there were three participants (see Method in main text) who had emotion recognition accuracy less than 50%. We conducted the analyses while excluding these participants and the results were the same. We found above chance level emotion recognition accuracy in both groups (TD: $t(22) = 9.575$, $p < .001$, $d = 2$; ASD: $t(24) = 7.756$, $p < .001$, $d = 1.6$), no difference between them (Effect of group: $F(1,46) = 0.193$, $p = .662$, $\eta_p^2 = .004$) and increased accuracy with emotion strength (Effect of intensity: $F(3,138) = 122.847$, $p < .001$, $\eta_p^2 = .728$). There was an Emotion*Group: interaction ($F(1,46) = 5.919$, $p = .019$, $\eta_p^2 = .114$) and within group analyses revealed the same results: better emotion recognition accuracy for fear as compared to anger specifically in TD but not in ASD (Effect of emotion, TD: $F(1,22) = 5.420$, $p = .03$, $\eta_p^2 = .198$; ASD: $F(1,24) = 0.567$, $p = .459$, $\eta_p^2 = .023$). Similarly, regarding the intensity ratings, there was an Emotion * Levels interaction ($F(3,138) = 88.138$, $p < .001$, $\eta_p^2 = .657$) but there was no interaction with Group ($F(3,138) = 0.850$, $p = .469$, $\eta_p^2 = .018$).

Lastly, as we our results including the three outliers we found no relationship between the explicit recognition of emotions and the interaction value of the participants in neither the TD ($R = .027$, $p = .902$) or the ASD group ($R = .123$, $p = .559$). Thus these 3 participants were included in the final analysis (see Results and Method sections in main text). The emotional intensity ratings for each group, while excluding those 3 participants, can be found in the Supplementary Table 1.

Supplementary Table 1. Mean (S.E.M.) emotional intensity ratings per group.

	Conditions	Level 1	Level 2	Level 3	Level 4
	Rating				
ASD N=25	Intensity (%) of anger	47 (2.3)	57 (2.7)	61 (2.4)	72 (2.3)
	Intensity (%) of fear	49 (3)	54 (2.6)	59 (2.6)	68 (2.4)
TD N=23	Intensity (%) of anger	46 (1.6)	57 (2)	62 (2)	71 (1.7)
	Intensity (%) of fear	47 (1.9)	57 (1.4)	61 (1.7)	65 (1.6)

Appendix 2: Kinematics recording and analysis (Experiment 2)

Throughout each trial movement kinematics were recorded using custom-made Matlab scripts. Using the Analyzer tool of Mousetracker software package (Freeman & Ambady, 2010) we extracted the temporal movement characteristics of interest (peak velocity, peak acceleration) to investigate whether there are interactions in velocity as expected from previous neurotypical adults results (Vilarem et al., under review). We adopted a regression-based approach, consisting of regressing the kinematic measures against the intensity (Wyart, Myers, & Summerfield, 2015; Wyart, Nobre, & Summerfield, 2012). We applied a general linear regression model (GLM) with intensity introduced as trial-by-trial predictors of the participants' peak acceleration. We calculated the corresponding regression parameter estimates for each participant and then averaged across them to produce group-level averages. Subsequently, we calculated the parameter estimates for the four conditions of interest and used the corresponding intercepts to perform a 2x2 repeated measures ANOVA on the peak velocity and acceleration with Emotion (anger vs. fear) and Side (away vs. toward) and Group (ASD vs. TD) as a between subject factor. Similarly to our RTs results the TD group made faster movements than the ASD group, as demonstrated by larger peak velocity (Effect of group: $F(1,54) = 4.332$, $p = .042$, $\eta_p^2 = .074$) and acceleration ($F(1,54) = 4.064$, $p = .049$, $\eta_p^2 = .07$). No other effects/interaction/comparisons were significant neither between nor within groups (velocity all $p > 0.25$, see Figure 19; acceleration all $p > 0.26$, see Figure 20).

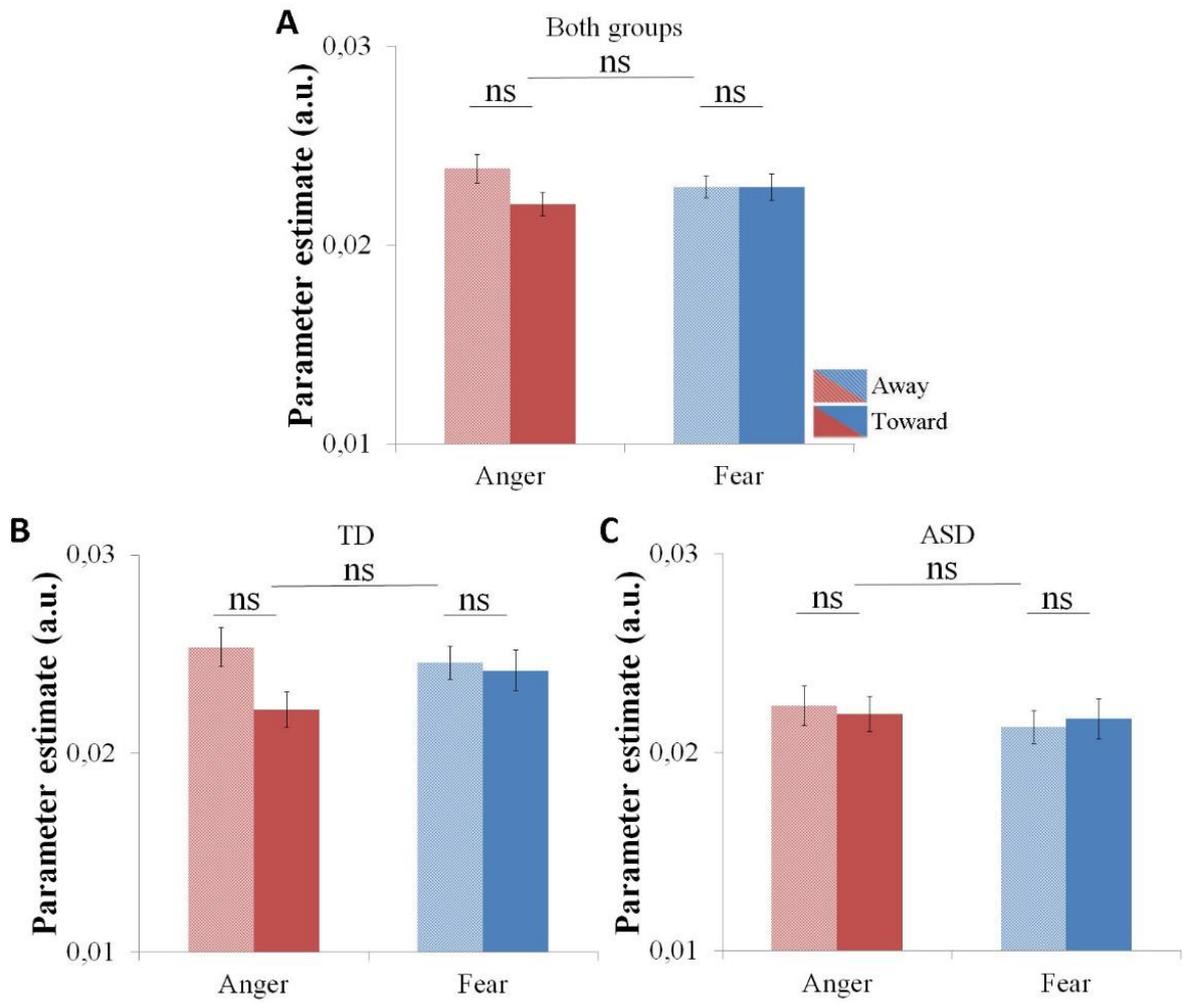


Figure 19 : A) Emotion-by-Side interaction on all participants' peak velocity, B) on the TD group's peak velocity and C) on the ASD group's peak velocity. Error bars represent Mean \pm S.E.M.; ns $p > 0.25$.

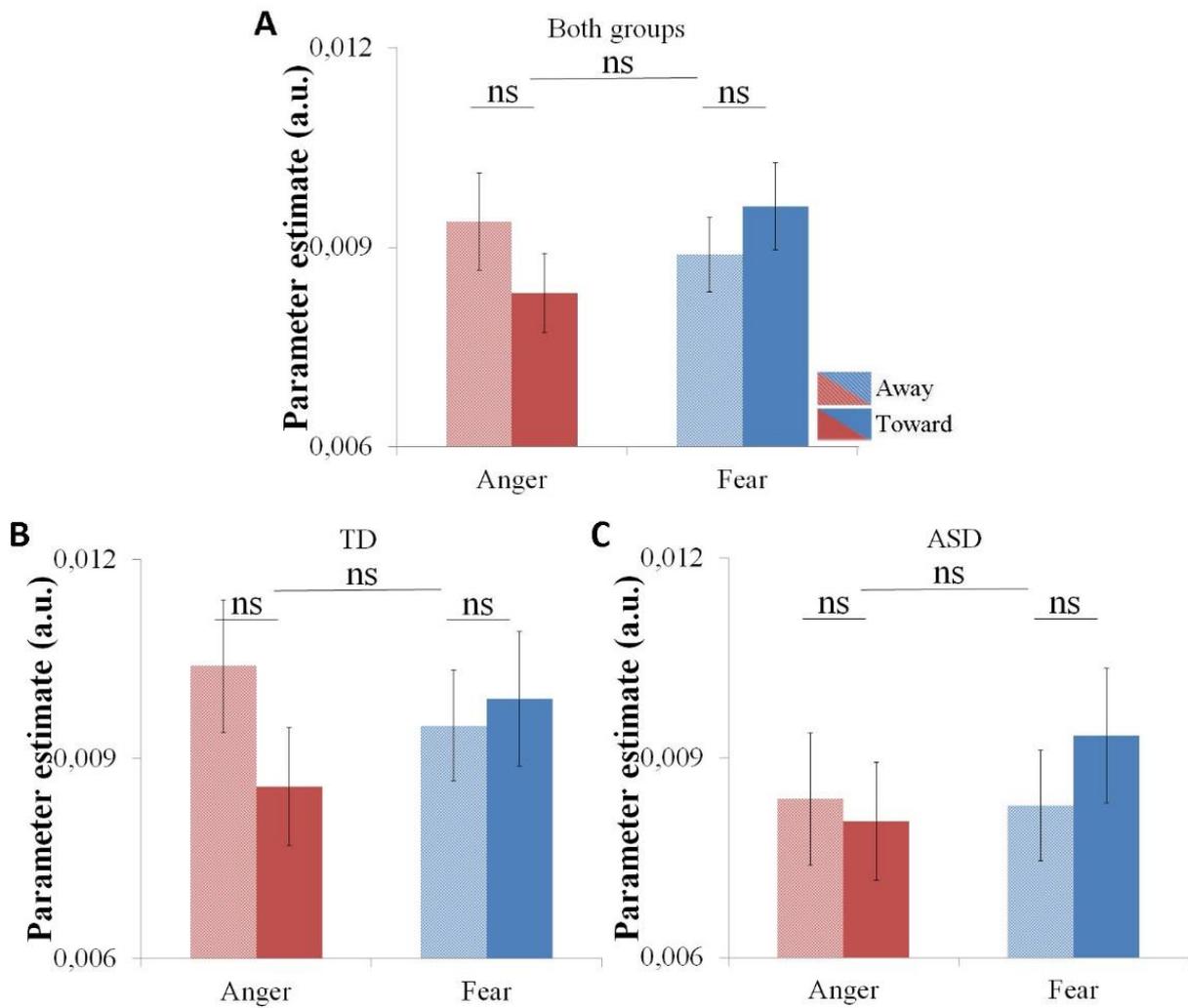


Figure 20 : A) Emotion-by-Side interaction on all participants' peak acceleration, B) on the TD group's peak acceleration and C) on the ASD group's peak acceleration. Error bars represent Mean \pm S.E.M.; ns $p > 0.26$.

Appendix 2: Eye-tracking recording and analysis (Experiment 2)

Throughout the study pupil data was recorded at 60 Hz sampling rate using the portable Eye Tribe tracker device, a developmental kit that has been found comparable to EYELINK 1000 for fixations and pupilometry (Dalmaijer, 2014). This tracker has a 0.5° accuracy (head free), a spatial resolution of 0.1° root-mean-square (RMS) and receives binocular gaze data, which it exports along the averaged values. For maximum efficacy the tracker was attached to the laptop under the screen at 40 cm distance from the participants' eyes. Participants completed a 9 point calibration of the EyeTribe developmental kit before each task (free action choice and explicit emotion categorisation).

Pupil data pre-processing. Due to technical issues, eye-tracking data of only 24 ASD and 23 TD participants was recorded. All eye data pre-processing was performed using custom-made Matlab scripts. We identified the segments of quickly drifting pupil, both growing and shrinking, excluded the bad/unusable pupil data and smoothed the data using a moving average. Lastly, we performed interpolation of artefacts and suppression of slow fluctuations. Given that the two groups were not tested in the same place and in order to eliminate effects of luminance, a baseline of 500 ms before the appearance of the stimulus was taken at each trial. We identified the peak pupil dilation on which was between 1000-1700 ms after stimulus onset for the ASD group and 1300-2000 ms after stimulus onset for the TD group.

Importantly, the Eye Tribe's pupil size is given in arbitrary units, and not in millimetres, and we were surprised to discover negative values representing the participant's pupil size (see Figure 21). Having corrected for baseline differences we are unsure whether such variance is justified and whether the data is meaningful and we cannot seek support because the company does not exist anymore. For the above reasons and given recent reports that, although the Eye Tribe is comparable to EYELINK 1000 (Dalmaijer, 2014), both systems when used remotely (portable) present large problems (Niehorster, Cornelissen, Holmqvist, Hooge, & Hessels,

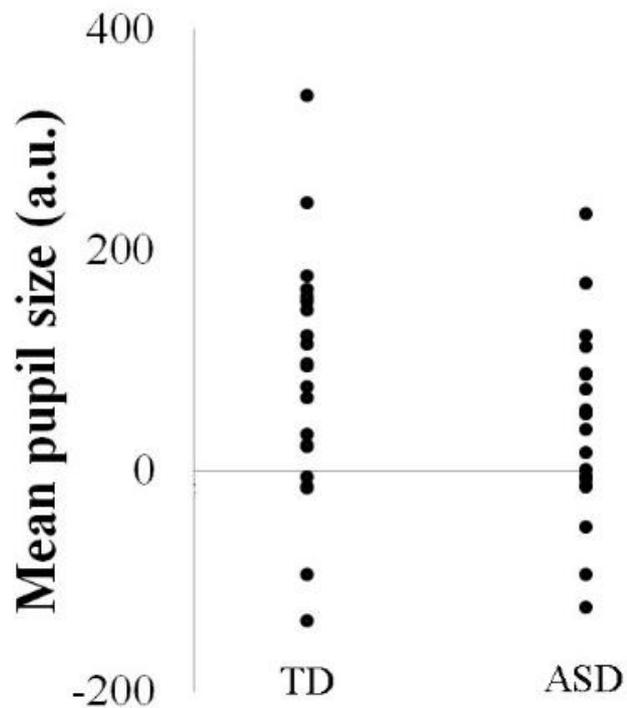


Figure 21 : Example mean pupil size values for TD and ASD participants after baseline correction.

2017), we decided to exclude the pupil data from further analysis.

Appendix 3: Distinct effects of social motivation on face evaluations in adolescents with and without autism (Experiment 3)

Distinct effects of social motivation on face evaluations in adolescents with and without autism

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Abstract

Social motivation is a personality trait that varies in clinical and non-clinical populations and that can thus be investigated across conditions in a dimensional framework. In the present paper, we tested whether social motivation had a similar impact in the general population and in a neuropsychological condition characterized by diminished social motivation: Autism Spectrum Disorders (ASD). More precisely, we evaluated the effect of social motivation on face evaluations on 20 adolescents with ASD and 20 matched controls using avatars parametrically varying in dominance and trustworthiness. In line with previous research, we found that social motivation was associated with a larger weight granted to perceived trustworthiness to produce likeability judgments in the control group. However, this pattern was not found in the ASD group. Importantly, this difference was not explained by differences in basic face processing skills. Social motivation thus appears to have a different effect in ASD and control populations, which raises questions about relying on subclinical or non-clinical populations to understand ASD.

Introduction

Compared to many other animals, humans stand out when it comes to a variety of social interactions they pursue and the importance of social activities in their ecological niche (Kaplan, Hooper, & Gurven, 2009). Consequently, the willingness to be included in social interactions and the propensity to preferentially attend to the social world is present early on in development and remains a driving force throughout the lifespan (Baumeister & Leary, 1995; Epley & Schroeder, 2014; Vouloumanos, Hauser, Werker, & Martin, 2010). Yet, individuals vary in the degree to which they are socially motivated both in the general population (Brown, Silvia, Myin-Germeys, & Kwapil, 2007; Germine, Garrido, Bruce, & Hooker, 2011; Gooding & Tallent, 2003; Kwapil et al., 2009) and in a number of clinical conditions (Chevallier, Kohls, et al., 2012; Harvey, Bodnar, Sergerie, Armony, & Lepage, 2009).

Recent developments in psychiatry (the Research Domain Criteria Framework) emphasise the need to investigate variations in relevant biological traits across clinical and non-clinical populations (Cuthbert, 2014; Insel et al., 2010; Sanislow et al., 2010); NIMH Strategic Plan for Research, 2015). For instance, Parish-Morris et al. (Parish-Morris et al., 2013) have shown using such a dimensional approach that individual differences in social attention was a better predictor of face processing skills than Autism Spectrum Disorders (ASD) diagnosis. Recently, social motivation has been identified as one of a relevant biological trait to study in such a dimensional approach (National Advisory Mental Health Council Workgroup on Tasks and Measures for Research Domain Criteria, 2016).

Atypical social motivation is indeed an important characteristic of multiple conditions, including Autism Spectrum Disorders (ASD) (Chevallier, Grèzes, et al., 2012; Dawson, Meltzoff, Osterling, Rinaldi, & Brown, 1998; Klin, Lin, Gorrindo, Ramsay, & Jones, 2009), anorexia, schizophrenia and depression (Blanchard, Horan, & Brown, 2001; Watson, Werling, Zucker, & Platt, 2010). Attention to social stimuli is also thought to provide a starting point for the development of social abilities, such as face processing (Gliga & Csibra, 2007; Grelotti et al., 2002), and lack of social motivation might thus have cascade effects on other areas of social cognition. In ASD in particular, it has been argued that early deficits in social motivation and social reward responsiveness might have a long lasting impact on social skills (Chevallier, Kohls, et al., 2012; Klin, Jones, Schultz, & Volkmar, 2003; Mundy, 2003). Given its central role in multiple conditions, it seems highly relevant to use a dimensional approach in order to improve our understanding of social motivation.

Although the dimensional framework is appealing and potentially powerful, it is however possible that variations in single traits have a drastically different impact when taken in isolation than when combined in the context of psychiatric conditions. For instance, social anhedonia has been shown to have a different impact on social cognition in patients with schizophrenia, patients with depressive

disorders and healthy controls (Harvey et al., 2009; Olsen, Bjorkquist, Bodapati, Shankman, & Herbener, 2015). In the case of ASD, stereotypical interests, anxiety, sensory atypicalities or any number of frequent co-morbidities associated with autism might also influence the way diminished social motivation alters individual behaviour. The aim of this paper is to apply the insights of dimensional approaches to study social motivation in ASD by testing whether social motivation has a uniform effect on individuals with and without ASD (NIMH Strategic Plan for Research, 2015), . To investigate this question, we focused on face evaluation, which is key for social decision making (Todorov et al., 2015), and which is sensitive to variations in social motivation. Specifically, Safra et al (under review) have shown that highly socially motivated adults place more weight on perceived trustworthiness when producing likeability evaluations. Here, we asked 40 adolescents participants (20 typically developing adolescents and 20 adolescents with ASD) to rate faces on likeability using well-controlled stimuli varying parametrically in dominance and trustworthiness (Figure 1A; Oosterhof and Todorov, (Oosterhof & Todorov, 2008). Our prediction was that higher levels of social motivation would increase the weight granted to trustworthiness during face evaluations in both TD and ASD populations.

Results

Cue processing in the TD and ASD groups. As our measure relied on the processing of facial features, we first checked that both groups were able to accurately detect and combine facial cues. Replicating previous findings (Cogsdill, Todorov, Spelke, & Banaji, 2014; Ewing, Caulfield, Read, & Rhodes, 2015b), TD adolescents successfully detected trustworthiness ($b = 0.19 \pm 0.03$, $t(579) = 13.947014$, $p < .001$) and dominance cues ($b = 0.16 \pm 0.03$, $t(579) = 10.93$, $p < .001$), giving higher ratings to avatars presenting higher levels of each trait. Similarly, in line with previous studies (Ewing, Caulfield, Read, & Rhodes, 2015a; Philip et al., 2010; White et al., 2006) adolescents with ASD successfully gave ratings that vary with avatar's level of trustworthiness and dominance ($b = 0.18 \pm 0.03$, $t(579) = 10.14$, $p < .001$; $b = 0.07 \pm 0.05$, $t(579) = 2.81$, $p = .005$).

Based on Oosterhof and Todorov (Oosterhof & Todorov, 2008) and Safra et al. (under review), we then reconstructed participants' likeability two-dimensional space based on their ratings of dominance and trustworthiness. As can be seen in Figure 1B, both adolescents with and without ASD combined perceived dominance and perceived trustworthiness to form likeability judgments such as, in both groups, more trustworthy and less dominant faces were rated as more likeable (TD group: $b_{Trustworthiness} = 0.47 \pm 0.07$, $t(575) = 13.27$, $p < .001$; $b_{Dominance} = -0.32 \pm 0.07$, $t(575) = -9.69$, $p < .001$; ASD group: $b_{Trustworthiness} = 0.52 \pm 0.07$, $t(575) = 14.03$, $p < .001$; $b_{Dominance} = -0.07 \pm 0.07$, $t(575) = -1.87$, $p = .062$).

Impact of social motivation in TD adolescents. We then examine whether, as in adults, social motivation increased the weight granted to trustworthiness for likeability evaluations in TD adolescents. As expected, social motivation increased the relative weight granted to trustworthiness for evaluating faces' likeability ($b_{SocMot*Trust} = 0.08 \pm 0.08$, $t(570) = 2.06$, $p = .039$; Figure 1B). Importantly, this effect was still present after controlling for physical and other motivations ($b_{SocMot*Trust} = 0.18 \pm 0.11$, $t(560) = 3.24$, $p = .001$). In addition, higher levels of social motivation were also associated with lower sensitivity to high levels of dominance ($b_{SocMot*Dom^2} = 0.14 \pm 0.12$, $t(570) = 2.41$, $p = .016$; after controlling for physical and other motivations: $b_{SocMot*Dom^2} = 0.11 \pm 0.10$, $t(560) = 2.29$, $p = .023$) as well as with a lower sensitivity to dominance ($b_{SocMot*Dom} = 0.06 \pm 0.07$, $t(570) = 1.71$, $p = .088$; after controlling for physical and other motivations: $b_{SocMot*Dom} = 0.13 \pm 0.15$, $t(560) = 1.67$, $p = .098$; all other effects, $p > .108$).

Because social motivation was associated with an increase in the perceived intensity of trustworthiness ($b = 0.03 \pm 0.03$, $t(578) = 2.01$, $p = .045$; all other effects on cue detection: all $ps > .104$), we conducted a similar model using avatars' objective cues of dominance and trustworthiness as predictors of likeability evaluations in order to check that the evidenced difference was not due to

this cue processing difference. This analysis confirmed that social motivation was associated with a larger weight granted to trustworthiness for likeability evaluations ($b_{SocMot*Trust} = 0.03 \pm 0.01$, $t(570) = 3.42$, $p < .001$; after controlling for physical and other motivations: $b_{SocMot*Trust} = 0.03 \pm 0.02$, $t(560) = 3.345240$, $p < .001$; no other significant effect of social motivation: all $ps > .124$). As a conclusion, social motivation had a similar impact in adolescents as in adults (Safra et al., under review).

Effect of social motivation in ASD. Applying the dimensional framework to the study of ASD, we then tested whether social motivation had a uniform impact across populations by analyzing the ASD and TD groups together and including Group (ASD vs TD) as a regressor. The interaction between social motivation and the weight granted to trustworthiness was different in the two groups ($b_{Group*SocMot*Trust} = -0.17 \pm 0.15$, $t(1140) = -2.18$, $p = .029$; no other difference in the effect of social motivation between the two groups was evidenced: all $ps > .127$), such that social motivation was not associated with an increased weight granted to trustworthiness in the ASD group ($b_{SocMot*Trust} = 0.05 \pm 0.11$, $t(1140) = 0.97$, $p > .250$). Importantly, controlling for the other two types of motivation (physical and other) confirmed this difference between groups ($b_{Group*SocMot*Trust} = -0.38 \pm 0.21$, $t(1120) = -3.47$, $p < .001$; no other significant effect of social motivation: all $ps > .250$) and revealed that social motivation was associated with a decrease in the weight granted to trustworthiness for likeability evaluations in the ASD group ($b_{SocMot*Trust} = -0.10 \pm 0.09$, $t(1120) = -2.17$, $p = .031$). In summary, social motivation does not have a uniform effect across the TD and the ASD groups.

In line with this finding, while the ASD group was less socially motivated than the TD group ($t(38) = -2.43$, $p = .019$), the comparison of these two groups did not match the difference between lowly and highly socially motivated adolescents without ASD. More precisely, compared to TD adolescents, adolescents with ASD perceived dominance cues as less intense ($b = -0.09 \pm 0.06$, $t(1158) = -3.04$, $p = .002$; no other significant difference in cue detection: all $ps > .250$), and granted less weight to dominance for evaluating likeability ($b_{SocMot*Dom} = 0.26 \pm 0.10$, $t(1150) = 5.03$, $p < .001$; no other significant effect of diagnosis: all $ps > 0.113$). Importantly, this effect was preserved while taking objective cues of dominance and trustworthiness for predicting likeability evaluations ($b_{SocMot*Dom} = 0.05 \pm 0.02$, $t(1150) = 4.62$, $p < .001$), indicating that the weighting difference between the ASD and TD groups could not be explained by differences in cue detection.

Discussion

The aim of this study was to assess whether social motivation had a similar impact in adolescents with and without ASD. Previous work had demonstrated that higher levels of social motivation increases the weight granted to trustworthiness cues during likeability evaluations (Safra et al., under review). We replicated this effect in TD adolescents. However, social motivation had the opposite effect in the ASD and was associated with a decrease in the weight granted to trustworthiness. This shows that social motivation can have contradicting effects in clinical and a non-clinical populations. While the ASD group was less socially motivated than the TD group, it would be tempting to construe autism as a simple case of extreme diminished social motivation and to use findings on low social motivation in the general population as a guide to predict ASD cognition. Instead, we found that participants with ASD displayed decreased sensitivity to dominance cues and granted less weight to dominance during likeability evaluations.

These findings have a range of implications for the understanding and investigation of ASD. First of all, our results suggest that the effect of social motivation uncovered in non-clinical populations cannot always be applied to ASD. Social disinterest in ASD may indeed be associated with emergent properties that cannot be derived by simply extrapolating the effects of mildly diminished social motivation. In addition, long-lasting difficulties in social interactions may have a retroactive action on social behaviour (Chamberlain, Kasari, & Rotheram-Fuller, 2006; Kasari, Locke, Gulsrud, & Rotheram-Fuller, 2010; Locke, Ishijima, Kasari, & London, 2010; Shattuck, Orsmond, Wagner, & Cooper, 2011). Finally, ASD are well-known for being associated with other conditions such as social anxiety and hyperactivity disorders (Matson & Nebel-Schwalm, 2007; Simonoff et al., 2008) that may interact with social motivation and give rise to second-order atypicalities. In this context, it is important to underline that findings obtained in subclinical populations or in non-clinical populations should be applied to ASD with a great deal of caution.

More widely, our results are relevant for dimensional approaches in psychiatry (Insel et al., 2010; Sanislow et al., 2010), NIMH Strategic Plan for Research, 2015). A growing body of research has indeed emphasized the importance of studying the impact of specific traits on behaviour by pooling clinical and non-clinical populations (Parish-Morris et al., 2013). However, our results suggest that findings obtained in non-clinical samples cannot always be directly mapped onto clinical populations. As suggested for the case of social motivation, it is indeed possible that variations in specific traits affect behaviour non-linearly or that co-morbidities interact to produce emergent symptoms. In addition, clinical thresholds may also have an intrinsic value in terms of cognitive functioning and biological traits may not always be good proxies to investigate psychiatric conditions. In this line of idea, it has been

shown that variations in overall anhedonia has different neural consequences in patients with schizophrenia vs. in control populations (Dowd & Barch, 2010). Similarly, social anhedonia has a different effect on emotional memory in patients with major depressive disorders, in patients with schizophrenia and in healthy controls (Harvey et al., 2009; Olsen et al., 2015). However, it is worth noting that multi-dimensional diagnostic measures such as the Autism Quotient may not present similar issues and findings relying on such measures in non-clinical populations may accurately predict atypicalities in ASD (Neufeld et al., 2016; Panasiti, Puzzo, & Chakrabarti, 2015).

Regarding the present study, we also wish to underline two potential sources of noise. First, self-reports of social motivation might be biased differently in the ASD and the TD group: individuals with ASD indeed have difficulties reporting their own feelings and may lack insight (Lombardo, Barnes, Wheelwright, & Baron-Cohen, 2007; Lombardo & Baron-Cohen, 2010, 2011); conversely TD participants are more likely to be susceptible to social desirability effects (Chevallier, Molesworth, et al., 2012). Our results should thus be replicated using more objective measures of social motivation (Chevallier et al., 2016; Dubey, Ropar, & Hamilton, 2015). Second, it is widely recognised that autism should not be construed as a unique neuropsychological condition and that a composite view is needed in order to take into account the existence of multiple endophenotypes in ASD (Happé et al., 2006; Jeste & Geschwind, 2014). It is thus possible that adolescents in our study belong to different subtypes of ASD that are characterized by different levels of social motivation deficits. Our results should thus be replicated on a much larger sample size, to identify whether social motivation has different effects in different subtypes of ASD.

Despite these caveats, we believe that our results are relevant for the understanding of social processing in ASD. In particular, we demonstrated that individuals with ASD are able to detect dominance and trustworthiness cues and to combine these cues to produce likeability evaluation (albeit differently from TD participants). These results are in line with a growing body of evidence showing preserved abilities to detect and to combine social cues in individuals with ASD (Caulfield et al., 2016, 2014; Ioannou et al., 2017; Philip et al., 2010; White et al., 2006). In addition, our study also extends previous results on social cues combination by showing that individuals with ASD are not only able to modulate their perception of faces by integrating different social signals but also that they are able to create new social judgments by combining social cues. Indeed, the detection of dominance and trustworthiness cues and their combination are processed in distinct brain regions (Todorov & Engell, 2008; Todorov, Said, Oosterhof, & Engell, 2011; Vecchiato et al., 2014).

Moreover, the impact of ASD on the way social cues are combined to produce likeability evaluations is particularly robust. Differences in likeability evaluations indeed remained after

controlling for participants' decreased sensitivity to dominance cues, which demonstrates an actual difference in dominance salience when producing likeability evaluations. Overall, our results thus suggest that individuals with ASD are able to detect and use dominance, but that they place less weight on this trait compared to TD individuals. Why that might be the case is an empirical question in need of further investigation. Nevertheless, a number of experiments have revealed that more masculine individuals are less sensitive to dominance (Watkins, Jones, & DeBruine, 2010; Watkins, Quist, Smith, DeBruine, & Jones, 2012). Therefore, our results may be in line with the previous research showing an exaggerated male pattern of neural activation in ASD during face evaluation (Hall et al., 2012).

To summarise, our study replicates previous findings obtained in healthy adults showing that social motivation increases the weight granted to trustworthiness to produce likeability judgments. In contrast with our prediction however, social motivation did not have the same impact in ASD and in TD. Despite an overall diminished social motivation in the ASD group, the impact of autism was quite different than the simple effect of social motivation in TD adolescents. This result suggests that it may be misleading to construe social motivation in isolation and that it is vital to further understand how social motivation interacts with other dimensions of ASD.

Method

Participants

A minimum target of 20 TD adolescents and 20 adolescents with ASD was fixed *a priori*. The exact number was determined by scheduling constraints. A final number 22 TD adolescents (6 females) and 22 adolescents with ASD (4 females), aged between 12 and 17 years old (TD: $M = 13.70 \pm 0.61$; results are given in the standard form: mean \pm 95% confidence intervals; ASD: $M = 14.45 \pm 0.89$), participated in this study. The experiment was approved by the local research ethics committee (ClinicalTrials.gov Identifier: NCT02628808, Protocol Study ID: 2008-A00019-46). The TD adolescents were recruited from a mainstream school and the adolescents with ASD were recruited from the University Hospital Robert Debré. The adolescents with ASD had received an official diagnosis of autism by an independent clinician according to the criteria of the Diagnostic and Statistical Manual for mental disorders-IV (DSM IV, (*Diagnostic and Statistical Manual of Mental Disorders, 4th Edition, Text Revision (DSM-IV-TR)*, 2000)). The Autism Diagnostic Interview Revised (ADI-R, (C. Lord et al., 1994)) and the Autism Diagnostic Observational Schedule (ADOS, (C. Lord et al., 2000)) were used to further assess the ASD group. The mean ADOS score for the ASD group was 13.59 ± 1.81 . All participants with ASD had normal vision (Freiburg Visual Acuity and Contrast Test version 3.8.2, (M. Bach, 1996) adapted to the distance used in the experiment of 0.3 meters), no participant was on medication during the period of the study. Preliminary interviews confirmed that TD adolescent participants did not have any special needs or history of psychiatric illness and all of them had normal or corrected to normal vision.

Before the testing, all parents and children provided their written informed consent for participating to the study. IQ was measured using the full Wechsler Intelligence Scale for Children version IV (WISC IV, (Wechsler, 2003); Mean = 103.40 ± 10.86 ; range: 70 - 148) in adolescents with ASD and with the French Wechsler Abbreviated Scale of Intelligence in TD adolescents due to time constraints (in the four subsets form as it has been shown to give the most representative score of the full IQ, (Grégoire, 2009); range: 87 - 138). Finally, at the end of the experiment, participants completed the Kazdin's Pleasure Scale (Kazdin, 1989), a self-rated questionnaire to assess their levels of anhedonia (see description below). In addition, trait anxiety was assessed using an abbreviated form of the State-Trait Anxiety Inventory (STAI; (Fioravanti-Bastos et al., 2011; Spielberger, 1983b)).

Materials and design

The pleasure scale

The Kazdin Pleasure Scale for Children (three subforms: social, physical and other; (Kazdin, 1989); Table 1) was used to assess participants' anhedonia levels. This scale is a validated self-rated instrument to

measure anhedonia in both children with and without ASD (Chevallier, Grèzes, et al., 2012). It consists of 39 items pertaining to social (e.g., “You accidentally overhear your teacher telling the principal what a terrific student you are”), physical (e.g., “You are cycling down the street very fast while still in good control of yourself”) or other sources of pleasure (e.g., “On a Saturday night, you stay up watching television as long as you want”). Participants were asked to read each item out loud and to rate their feeling in the corresponding situation on a 3-point Likert scale (“Very happy”, “Happy” or “Neither happy nor unhappy”). The three scales were reverse-coded for the analysis in order to reflect participants’ levels of motivation.

The Face Evaluation Task

The experiment was programmed on EPrime (Psychology Software Tools, 2002) and lasted approximately 15 minutes. 30 faces varying parametrically on dominance and trustworthiness were generated using FaceGen 3.1 (<http://www.facegen.com>). Previous research has shown that these faces elicit dominance and trustworthiness judgments both at the explicit and the implicit level (Stewart et al., 2012; Todorov, Dotsch, Porter, Oosterhof, & Falvello, 2013). Following Oosterhof and Todorov’s methodology, the questions bearing on the three traits of interest, i.e. trustworthiness, dominance or likeability, were presented in separate blocks (Oosterhof & Todorov, 2008). The sequence of the three blocks and the sequence of trials within each block were randomized between blocks and between participants. Participants had to answer: “How [trait] is this person?” (“À quel point cette personne est-elle [trait]?”) using a cursor on a 9-point scale ranging from 1 “not at all [trait]” (“Pas du tout [trait]”) to 9 “extremely [trait]” (“Extrêmement [trait]”, recoded from -1 to +1 for the analyses). Depending on the block, [trait] was replaced with “trustworthy” (“digne de confiance”), “dominant” (“dominant”) or “likeable” (“sympathique”). The face, the question and the scale appeared simultaneously on the screen. Participants were instructed to answer following their first impression and they were told that there was no right or wrong answer. The mouse was initially set to the middle of the screen in order to reinforce the salience of the positive and the negative sides of the scale. The name of the dimension was displayed in each trial (Figure 1A).

Procedure

Participants were tested individually in a quiet room. Participants were seated at 30 cm distance from the laptop. They completed three separate blocks of the face evaluation task, each block consisted of the same 30 faces. Participants could rest between each block. Following completion of the 90-trial experiment, participants filled out the STAI and the Kazdin Pleasure scale with the experimenter.

Data cleaning

2 TD participant and 2 ASD participants were excluded from the analysis for using only one side of the scales.

Group differences

We first checked that the included participants of the ASD and TD groups were matched on age, gender, IQ and anxiety. The ASD and TD groups did not differ on any of these variables (Table 1). We then measured the difference between the ASD and TD groups in the different types of motivation. As in previous studies (Chevallier, Grèzes, et al., 2012), the ASD group was significantly less socially motivated than the TD group ($t(38) = -2.43, p = .019$) but did not differ in the two other types of motivation (Table 1). However, it is worth noting that contrary to Chevallier et al. (2012), social motivation did not significantly correlate with ADOS severity scores (coded as indicated in (Gotham, Pickles, & Lord, 2009); $r = -.02 \pm 0.44, N = 20, t(16) = 0.09, p > .250$)

Finally, to test for possible differences between the ASD and the TD groups in the way participants performed the task, we ran several t-tests on scale use variables (i.e., ratings variance, number of different ratings, lower and higher ratings) for each scale. None of these values were significantly different between the two groups either for the dominance scale (all $ps > .250$), the trustworthiness scale (all $|t(40)| < 0.55, all ps > .250$) or the likeability scale (all $ps > .118$).

Data analysis

Cues decoding: To measure the influence of social motivation on participants' ability to decode trustworthiness and dominance cues, we ran mixed linear regressions on trustworthiness and dominance ratings, taking avatars' levels of trustworthiness / dominance as well as participants' level of social motivation as regressors and participants' ID as a random factor.

Likeability evaluations: To investigate the impact of social motivation on the composition of likeability judgments, we ran a mixed linear regression on likeability evaluations, taking social motivation, ratings of dominance and ratings of trustworthiness as predictors and participants' ID as a random factor. Following Todorov et al. (Todorov et al., 2011), this model included linear and quadratic interaction effects of perceived trustworthiness and perceived dominance as well as interaction terms between these two factors.

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Figures, tables and legends

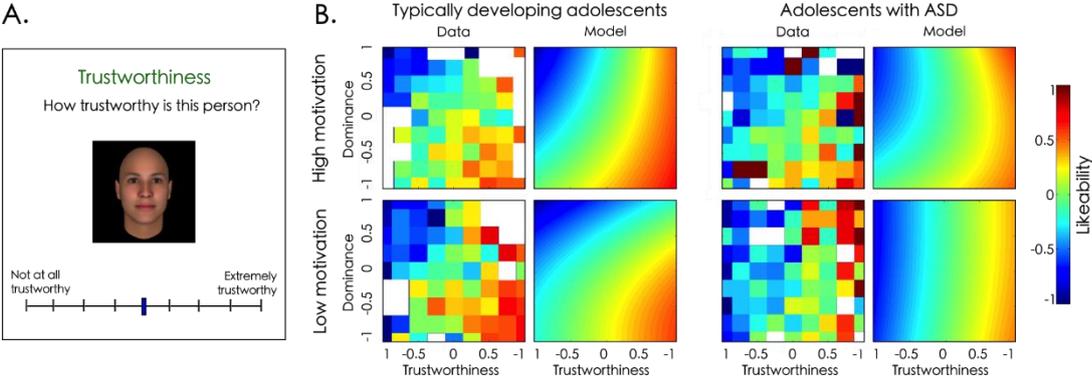


Figure 1: Social motivation has distinct effects on face evaluations in adolescents with and without ASD: (A) Example of an evaluation trial. Participants had to rate each face by moving a cursor. (B) Likeability ratings as a function of trustworthiness (x axis) and dominance ratings (y axis) for the typically developing adolescents (left) and the adolescents with ASD (right). Rating intensity is represented on a scale ranging from blue for lower ratings to red for higher ratings. Pixelated figures correspond to averaged data in the initial study (data) for the most (upper row) and least (lower row) socially motivated participants (median split). Smoothed figures represent the predictions of the regression models ran separately on the two participant samples. While in typically developing adolescents, higher levels of social motivation was associated with an increase in the weight granted to trustworthiness, this was not the case in adolescents with ASD.

Table 1 - Descriptive statistics for age, gender and IQ and anxiety of the ASD and TD groups

	TD (N = 20)	ASD (N = 20)	Statistics
Age	13.70 ± 0.61	14.00 ± 0.88	$t(38) = 0.58, p > .250$
Gender ratio	25 % female	15 % female	$\chi^2(2, N = 42) = 0.00, p > .250$
IQ	106.60 ± 6.14	100.85 ± 10.13	$t(38) = -1.02, p > .250$
STAI	13.80 ± 1.80	14.35 ± 1.96	$t(38) = 0.43, p > .250$
Social Motivation	30.10 ± 1.74	34.10 ± 2.97	$t(38) = -2.43, p = .019$
Physical Motivation	12.80 ± 0.91	13.10 ± 1.23	$t(38) = -0.41, p = .684$
Other Motivation	18.65 ± 2.06	21.15 ± 1.73	$t(38) = -1.94, p = .059$

Résumé

Les troubles du spectre de l'autisme (TSA) sont caractérisés par des difficultés persistantes dans les domaines de la communication et des interactions sociales. Les individus atteints de TSA ont notamment des difficultés à décoder les émotions d'autrui et il est souvent suggéré qu'un déficit général du traitement des visages émotionnels est à l'origine de ces difficultés. Cependant, les résultats de la littérature sont incohérents et soulignent l'importance de facteurs méthodologiques qui pourraient influencer la performance des personnes TSA. Deux théories actuelles sont pertinentes au regard de ces difficultés rencontrées dans les interactions sociales : 1) la théorie de la régulation comportementale propose que ces difficultés résultent de dysfonctionnements du traitement des émotions et/ou des mécanismes permettant de répondre de façon appropriée à ces émotions; et 2) la théorie de la motivation sociale propose au contraire que ces mécanismes sont intacts et que les difficultés rencontrées sont le résultat d'un déficit de motivation sociale. Cette thèse avait pour but de départager ces deux théories, tout en contrôlant de nombreux facteurs méthodologiques qui pourraient influencer la performance des personnes TSA. L'expérience 1 visait à étudier l'impact de la direction du regard sur le traitement de la peur et de la colère. L'expérience 2 étudiait les choix d'actions spontanées en présence de visages de peur ou de colère et la catégorisation de ces émotions présentées en vision périphérique. Ces deux études révèlent des résultats similaires chez des adolescents neuro-typiques et TSA. Ces deux groupes sont capables de décoder des expressions de peur et de colère, présentées au centre de l'écran ou en périphérie, ils sont aussi sensibles aux variations d'intensité de ces émotions et aux variations de contexte (ici étudié sous la forme de la direction du regard). D'autre part, les deux groupes répondent de façon similaire à ces émotions, notamment en choisissant des actions qui leur permettent d'éviter des individus menaçants. Pris dans leur ensemble, ces résultats indiquent que les mécanismes impliqués dans le traitement des émotions, l'intégration des facteurs contextuels, et dans l'adaptation de son comportement en réponses à ces signaux sociaux sont intacts chez des adolescents atteints de TSA. Ces résultats sont discutés au regard des théories de la motivation sociale et de la régulation comportementale.

Mots Clés : autisme, menace sociale, prise de décisions, tendances d'action, adolescents, modèles computationnelles.

Abstract

Autism spectrum disorders (ASD) are neurodevelopmental conditions characterised by persistent deficits in social reciprocity. Deficits in emotion perception are common in ASD and suggested to stem from a generalised deficit in the processing of facial affect. The literature however is inconsistent, stressing the importance of methodological factors that might bring individuals with ASD to a disadvantage. Two relevant theoretical frameworks are considered: 1) the behavioural self-regulation account proposes that affective atypicalities stem from deficits in the processing of the emotional signals and/or the regulation of appropriate responses to these signals; and 2) the social motivation account proposes that the mechanisms behind either of these two stages of emotion understanding are intact and that behavioural deficits stem from reduced weighting of social information. This Ph.D. aimed to disentangle between the two theories in the context of social threats by taking into account the necessary methodological factors. Experiment 1 investigated the contextual impact of gaze direction on the categorisation of facial expressions of anger and fear. Experiment 2 investigated both free action choice in response to implicit social threats –facial expressions of anger and fear- and their emotion categorisation accuracy in visual periphery. Across both studies ASD and typically developing (TD) adolescents demonstrated intact processing of both anger and fear in direct view and in visual periphery and were sensitive to the changes in emotional intensity of the stimuli. In Experiment 1, although the control group was overall more accurate than the ASD group in emotion decoding, gaze direction impacted the processing of threat similarly in both groups. Specifically, gaze direction raised the saliency of the threat for the observer and enhanced their sensitivity to the most salient ones. In Experiment 2, both groups demonstrated an overall tendency to avoid emotional agents, which was particularly evident in the case of anger. Taken together, the mechanisms behind the processing of facial social threats appear relatively spared in ASD adolescents and the impact of contextual factors are similar ASD and typical development. Adolescents with ASD are able to use social threats to adapt their behaviour by avoiding the emotional agent, which is not surprising during a developmental period characterised by enhanced reactivity to threat. These findings are discussed in terms of the social motivation and behavioural self-regulation frameworks and future directions are proposed.

Keywords: autism, social threat, decision making, action tendencies, adolescents, computational modelling.