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The recognition of emotional biological movement in individuals with typical development and Autism Spectrum Disorder (ASD)

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Contents

General introduction	1
The importance of the body motion	2
Why is useful to study the BM in individuals with Autism Spectrum Disorder.....	3
Chapter 1	6
THE COMPREHENSION OF BODY LANGUAGE: VISUAL PERCEPTION OF NEUTRAL AND EMOTIONAL WHOLE BODY MOVEMENTS IN INDIVIDUALS WITH AUTISM SPECTRUM DISORDER	6
Abstract	6
1.1. Introduction.....	7
1.2. Rating of the stimuli	10
1.2.1. Participants:.....	11
1.2.2. Stimuli:.....	11
1.2.3. Design and procedure:	12
1.2.4. Results:	14
1.3. EXPERIMENT 1: The recognition of emotional Point-Light and Full-light display in children with Autism Spectrum Disorder.....	14
1.3.1. Participants:.....	15
1.3.2. Analysis:	16
1.3.3. Stimuli:.....	17
1.3.4. Procedure:	17
1.3.5. Results:	18
1.3.5.1. Analysis of accuracy:.....	19
1.3.5.1.1. Within group comparison:.....	19
1.3.5.1.2. Between groups comparisons	22
1.3.5.1.3. Relation between Accuracy, IQ and age.....	25
1.3.5.2. Analysis of response times (RTs)	26
1.3.5.2.1. Within group analysis	27
1.3.5.2.2. Between groups analysis	28
1.3.5.2.3. Relation between RT, IQ and age	30
1.3.6. Discussion	32
1.3.6.1. Differences between Full-light and Point-light display of body movements	33
1.3.6.2. Differences across emotional contents	34
1.3.6.3. Relation between IQ, age and the recognition of body language.....	35
1.4. EXPERIMENT 2: How do adults with ASD recognize the emotional body language?.....	37

1.4.1. Introduction.....	37
1.4.2. Participants.....	39
1.4.3. Procedure	41
1.4.4. Results	41
1.4.4.1. Analysis of Accuracy	41
1.4.4.1.2. Within group analysis	41
1.4.4.1.3. Between group comparison	42
1.4.4.1.4. Regression model with IQ and accuracy	43
1.4.4.2. Analysis of response times (RTs)	44
1.4.4.2.1. Within group analysis	44
1.4.4.2.2. Between groups analysis	45
1.4.4.2.3. Relation between IQ and RTs	46
1.4.5. Discussion	47
1.5. The development of the ability to recognize the emotional meaning of Biological Motion: a comparison between children and adults in TD population and individuals with high functioning and low functioning Autism Spectrum Disorder.	50
1.5.1 Introduction.....	50
1.5.2 Results	53
1.5.2.1 Comparison between children and adults in TD group.....	54
Analysis of the Accuracy	54
Regressions.....	54
1.5.2.2. Comparison between children and adults with HF ASD.....	56
Analysis of Accuracy	56
Analysis of the RTs.....	56
Regression	56
1.5.2.3. Comparison between children and adults with LF ASD	57
Analysis of the RTs.....	57
Regression	57
1.5.3. Discussion	58
1.5.3.1 Interpretation of results in TD groups.....	58
1.5.3.2. Interpretation of results in ASD groups.....	60
Chapter 2	64
DEFICIT IN EMOTION RECOGNITION IN HIGH FUNCTIONING AUTISM SPECTRUM DISORDER: A COMPARISON BETWEEN FACIAL AND BODILY EXPRESSIONS.....	64

2.1. Introduction.....	64
2.2. Methods	71
2.2.1. Participants.....	71
2.2.2. Stimuli.....	72
2.2.2.1. Images of Body movements	72
2.2.2.1.1. Pilot study.....	73
2.2.2.2. Images of Facial expressions	74
2.2.2.3. Videos of point-light (PLDs) and full-light (FLDs) display.....	75
2.2.2.4. Final set of stimuli.....	75
2.2.3. Procedure	76
2.3. Results	77
2.3.1. Analysis of Accuracy	77
Between group comparisons.....	77
Within group comparisons	78
2.3.2. Analysis of Response Times (RTs).....	80
2.3.2.1. <i>The first research question we aimed to answer was whether there exist a difference in recognizing the emotions expressed by face or by body.</i>	81
Within group comparison:.....	81
Between group comparison	82
2.3.2.2. <i>The second research question we wanted to investigate was whether the vision of the body form, compared to the sight of pure motion information, could influence the time needed to identify the emotional content of body movements. In another words: "Is there any difference in RTs between FLDs and PLDs"?</i>	86
Within group comparison.....	86
Between group comparison	87
2.3.2.3. <i>Our third research question was whether there is a difference in recognizing the body expressions represented by dynamic or static stimuli. And also, is the perception of the actual movement important for better identify the different emotional meanings of body movements?</i>	89
Within group analysis	90
Between group comparison	91
2.4. Discussion	92
Chapter 3	99
MOTION OR E-MOTION? REPRESENTATION OF OBSERVED EMOTIONAL BODILY EXPRESSIONS IN THE ANTERIOR INTRAPARIETAL CORTEX AND SUPERIOR TEMPORAL SULCUS: A TMS STATE-DEPENDENT STUDY.....	99
Abstract	99

3.1. Introduction.....	100
3.2. Methods	106
3.2.1. Stimuli.....	106
3.2.1.1. Pilot experiment	107
Participants.....	107
Procedure	108
Pilot results.....	108
3.2.2. Behavioural Experiment	109
3.2.2.1. Behavioural Participants.....	109
3.2.2.2. Behavioural Procedure	110
3.2.2.3. Behavioural Analysis.....	111
3.2.3. TMS Experiment	113
3.2.3.1. TMS Participant	113
3.2.3.1. TMS settings and procedure.....	114
3.2.3.2. Neuronavigation	114
3.2.3.3. Identification of stimulation sites.....	115
3.2.3.4. Transcranial Magnetic Stimulation.....	116
3.2.3.5. TMS Analysis.....	117
3.2.3.6. TMS Results	118
3.3. Discussion	122
3.3.1. Interpretation of results in pSTS.....	123
3.3.2. Interpretation of results in aIPS.....	125
3.4. Conclusion	128
Chapter 4	129
GENERAL DISCUSSION	129
Aged-related changes in bodily emotion recognition	136
<i>Differences in body emotional valence recognition across different lighting conditions</i>	139
<i>The role of motor system in the emotion comprehension development</i>	143
<i>An out-of-tune chorus</i>	146
Bibliography.....	153

List of Figures

Figure 1	14
Figure 2	18
Figure 3	22
Figure 4	23
Figure 5	24
Figure 6	26
Figure 7	29
Figure 8	30
Figure 9	31-32
Figure 10	43
Figure 11	44
Figure 12	46
Figure 13	55
Figure 14	55
Figure 15	57
Figure 16	76
Figure 17	82
Figure 18	84
Figure 19	85
Figure 20	86
Figure 21	87
Figure 22	88
Figure 23	89
Figure 24	90
Figure 25	91
Figure 26	112
Figure 27	115
Figure 28	116
Figure 29	119
Figure 30	120

List of Table

Table 1	16
Table 2	27
Table 3	40
Table 4	71
Table 5	78
Table 6	121

General introduction

“Actions speak louder than pictures when it comes to understanding what other are doing and feeling”

Charles Darwin, 1872

The importance of the body language in social interaction

The human being is an extremely social animal and our life is continuously linked to that of our conspecifics. During the daily life, we constantly interact and communicate with other people, therefore the recognition of our interlocutors' identity and the comprehension of their actions, intentions, and emotions is crucial to successful social interaction. During the course of the evolution, the social animals have acquired a full range of interpersonal abilities to monitor their own and others' behaviours, and to react properly to social signals. Thanks to these abilities, humans can survive and successfully interact within the societies they belong to. The face is a main conveyer of this kind of information, leading the observer to easily infer the social relevant cues. This could be the reason why in the past decades the majority of the studies have mainly focused on face understanding (de Gelder, 2009; de Gelder et al., 2010). However, it is worth noticing that the correct perception of faces is complex and requests a proximity between the agent and the observer (Atkinson & Adolphs, 2011; Behrmann, Scherf, & Avidan, 2016; Haxby, Hoffman, & Gobbini, 2000; Tsao & Livingstone, 2008). On the other side, the body language is as efficient as face in conveying social relevant information, and it is clearly recognizable also when the observer is far from the agent and the face is not visible (de Gelder, 2006; de Gelder & Hortensius, 2014; Schindler, Van Gool, & de Gelder, 2008). Furthermore, in some occasion facial and bodily expression may provide different meanings, and in this case the body seems to play a pivotal

role in interpreting the emotional state of the observed people (Aviezer & Todorov, 2015; Kret, Roelofs, Stekelenburg, & de Gelder, 2013; Van den Stock, Righart, & de Gelder, 2007). Evolutionary speaking, the ability to interpret actions, emotions and intentions from a distance has a great utility, especially when the stimulus is threatening, because this allows us to promptly react to the external stimulus and to adopt the correct strategies for facing it (e.g. fight or flight) (Porges 1995; Bradley 2009). Thus, it becomes evident that the ability to properly elaborate the meaning of the human body movements is crucial for the comprehension of the social environment and, consequently, for implementing the right adaptive behaviours.

The importance of the body motion

Movement is a crucial feature in visual perception as the external environment is full of moving elements: some of them are living being (biological), while others are inanimate objects (non-biological). The biological and non-biological stimuli are defined by distinctive patterns of kinematic (Pollick, Paterson, Bruederlin, & Sanford, 2001; Roether, Omlor, Christensen, & Giese, 2009; Troje, Westhoff, & Lavrov, 2005) and the correct perception of these motion cues is fundamental for their identification. In particular, the human movement has specific motion characteristics that distinguish it from the motion of inanimate objects (Chouhourelou, Matsuka, Harber, & Shiffrar, 2006; Pollick et al., 2001; Troje, 2008; Troje et al., 2005). In 1973, the Swedish psychophysicist Gunnar Johansson introduced an innovative method to study the BM, the so called Point-light display (PLDs) (Johansson, 1973). These stimuli consist in few lighting dots reproducing the whole-body human movement, and are also referred as Biological Motion (BM) stimuli. The advantage offered by this technique is to isolate the information relative to the motion from all the other visual characteristics of the stimulus (such as colour, luminance, shape, etc.), allowing to investigate the contribution of motion signals to body

movement perception. Johansson's findings revealed that, despite the complete absence of forms and texture cues, naïve observers were able to readily interpret these few moving dots as a human walking figure (Johansson, 1973). Since this method has been introduced, a copious number of studies has showed that the perception of biological motion represented by point-light display is sufficient for inferring a great amount of social information: neurotypical individuals can easily recognize identity (Kozlowski & Cutting, 1977; Troje et al., 2005), gender (Johnson, McKay, & Pollick, 2011; Kozlowski & Cutting, 1977; Pollick, Lestou, Ryu, & Cho, 2002), the nature of the actions (Alaerts, Nackaerts, Meyns, Swinnen, & Wenderoth, 2011; Dittrich, 1993; Johansson, 1973), intentions (Roché et al., 2013) and emotions (Atkinson, Dittrich, Gemmell, & Young, 2004; Clarke, Bradshaw, Field, Hampson, & Rose, 2005; Dittrich, Troscianko, Lea, & Morgan, 1996; Roether et al., 2009). Taken together, those studies suggest that the motion itself is a rich source of information and it conveys a great amount of socially relevant meanings.

Why is useful to study the BM in individuals with Autism Spectrum Disorder

The Autism Spectrum Disorder is characterized by deficit in social interaction, which is pervasive and also present in people with high-level of cognitive resources (American Psychiatric Association, 2013). For this reason, research involving this population offers the precious opportunity to better understand the role played by the body perception and body movement comprehension in social cognition. In the last decade, the perception of BM in individuals with ASD has been increasingly investigated. Results of those studies suggested that the social difficulties in ASD might partially be linked to an impairment in processing and understanding the biological motion information (Kaiser et al., 2010; Mcpartland, Coffman, & Pelphrey, 2012; Pavlova, 2012), which seems to be present since early in development (Pelphrey, K. A., Shultz, S., Hudac, C. M. & Vander Wyk, 2012). Indeed, it has been shown that 2-years

old children with ASD failed to orient to BM stimuli (Klin, Lin, Gorrindo, Ramsay, & Jones, 2009). Accordingly, the neural structure underling the BM processing have been reported to develop differently in individuals with ASD and TD control (Alaerts et al., 2014; Freitag et al., 2008; Herrington et al., 2007; Kaiser & Shiffrar, 2009; McKay et al., 2012). The BM perception has mostly being studied using PLDs representing the human walking embedded in masking dots or compared to scrambled stimuli (see Pavlova 2012; Simmons et al. 2009 for reviews). Those researches has reported deficit in people with ASD in identifying the BM pattern of movements. Furthermore, the recognition of emotional PLDs has unanimously been found to be impaired in ASD, either in children, adolescents, and adults (Atkinson, 2009; Hubert et al., 2007; Moore, Hobson, & Lee, 1997; Nackaerts et al., 2012; Parron et al., 2008). However, in tasks requiring an explicit categorization of PLDs depicting neutral actions, research in ASD have provided conflicting results (Annaz, Campbell, Coleman, Milne, & Swettenham, 2012; Freitag et al., 2008; Moore et al., 1997; Murphy, Brady, Fitzgerald, & Troje, 2009). This heterogeneous findings might be due to several factors, such as the adopted matching criteria with the control group, the variability in ASD's cognitive profiles, the age of participants, the types of stimuli, or the task. Furthermore, it is important to notice that the greatest majority of those studies has been conducted including participants with high-functioning ASD (HF ASD), and very little is known about the recognition of neutral and emotional BM in people with low-functioning ASD (LF ASD). This “HF ASD-bias” could have contributed in drawing partial conclusion regarding the BM perception, as individuals with ASD with high-level of cognitive resources might develop and adopt compensatory mechanisms which help them to compensate their difficulties. This could explain the absence of differences between ASD and typically developing population reported by some studies, especially with adult participants.

Another issue is that when participants are children results are even less constant, due to the variability of ages and thus of their stage of development.

During my PhD I have investigated the ability to comprehend of the emotional valence of body movements in individuals with ASD. In Chapter 1, I will explain three different experiments where I compared the recognition of pure motion stimuli with more naturalistic representation of body actions (showing also the body form). I have explored this abilities both in children and adults with ASD with respect to TD controls, using the non-verbal IQ as matching criteria and asking participants to perform a non-verbal matching task. In Chapter 2, I investigated whether the impairment in individuals with ASD was restricted to the comprehension of body movements or widespread to other social cues (such as faces). Furthermore, I have compared static and dynamic representations of bodily expressions to explore the contribution of dynamic information in determining the deficit in body movement recognition. Finally, in Chapter 3 I will present a behavioural and a TMS studies aimed to explore the existence of a mechanism specific for the recognition of the emotional valence of body movements and the neural areas underlying it.

Chapter 1

THE COMPREHENSION OF BODY LANGUAGE: VISUAL PERCEPTION OF NEUTRAL AND EMOTIONAL WHOLE BODY MOVEMENTS IN INDIVIDUALS WITH AUTISM SPECTRUM DISORDER

Abstract

The biological motion (BM) includes the movement of face, body and eye gaze. It conveys social meaning and its correct elaboration is crucial to social cognition and social interaction. The traditional stimuli used to study human biological motion perception are the so-called point-light displays (PLDs), introduced by Johansson (Johansson, 1973). To date, conflicting results have been reported regarding the processing of BM in individuals with Autism Spectrum Disorder (ASD). Using neutral PLDs, some studies have found an impairment associated with ASD while others have not. Besides, deficits in emotion recognition in young children, adolescents, and adults with ASD are consistently reported when emotional PLDs are used. In the present Chapter, I will present three studies that we have realized using Atkinson's movies (Atkinson et al., 2004; Atkinson, Vuong, & Smithson, 2012) to investigate whether ASD show deficits in emotion recognition or not, across different stimulus display types (Point-light and Full-light display). The three studies involved individuals with ASD with different levels of functioning and typically developing controls (TD), matched for chronological age and non-verbal IQ level. In Experiment 1 we compared the ability to recognize the emotional valence of whole-body movement in children with low functioning ASD (LF ASD), high functioning ASD (HF ASD) and TD controls. In the Experiment 2, we have investigated the same ability in adults with LF ASD, HF ASD and TD controls. In the Experiment 3, we have compared the performance of children and adults in all the three groups to investigate the existence of differences in the developmental trajectory of this ability.

In general, we found an impairment in the ASD groups in recognizing both neutral and emotional movements, related with age and non-verbal IQ. Furthermore, results showed that happy movements were less recognizable than fearful and neutral, both in children and adults. Finally, FLDs were recognized faster and more accurately than PLDs in TD participants but not in participants with ASD.

1.1. Introduction

The Autism Spectrum Disorder (ASD) is a neurodevelopmental disorder characterised by “Persistent deficits in social communication and social interaction across multiple contexts”, “Deficits in social-emotional reciprocity” and “Deficits in nonverbal communicative behaviours used for social interaction” (American Psychiatric Association, 2013). In the last decade, it has been proposed that this impairment could be associated with difficulties in biological motion (BM) processing (Kaiser et al., 2010; Pavlova, 2012). Indeed, the moving human body is rich of others’ attitudes cues and the correct perception and interpretation of other people’s feelings is fundamental for social interaction. The ability to understand the emotional meaning of gestures and actions performed by other people, and consequently to react to them in a proper way, are the basis for the social reciprocity. The importance of this ability is also reflected at the neural level: in typically developing (TD) people, human motion is interpreted by a specific neural circuit, in which the posterior part of the superior temporal sulcus (pSTS) plays a leading role (Adolphs, 1999; Pelphrey & Morris, 2007; Puce & Perrett, 2003). Across the lifespan, the sensitivity of this area to BM increases relative to non-biological motion (i.e. object movement) (Carter & Pelphrey, 2006a), but this progressive tuning seems not to happen in people with ASD (Vértes & Bullmore, 2015). Deficiency in social interaction has been reported very early in the development of children with ASD (Klin & Jones, 2008; Klin et al., 2009) and it has been proposed to be associated with deficits in processing the information conveyed by the body movements (Dakin & Frith, 2005; Kaiser et

al., 2010; Mcpartland et al., 2012; Pavlova et al., 2005). Individuals with ASD often fail to figure out the meaning of gestures and show anomalous patterns of brain activation during motion perception (Freitag et al., 2008; Herrington et al., 2007). However, the existence of a deficit in BM perception in ASD population is still debated in literature, as some studies failed to find differences between neurotypical population and people with ASD in recognizing PLDs of neutral movements (Hubert et al., 2007; Moore et al., 1997; Murphy et al., 2009; Parron et al., 2008; Saygin, Cook, & Blakemore, 2010a). On the contrary, the ability to recognize the emotion has always been reported as impaired in ASD population, especially when conveyed by biological motion (Alaerts et al., 2014; Atkinson, 2009; Hubert et al., 2007; Moore et al., 1997; Nackaerts et al., 2012; Parron et al., 2008; Philip et al., 2010).

To clarify the comprehension of emotional movements in people with ASD may help to better understand how they perceive the social world around them, and hence to explain the origin of the difficulties encountered in everyday interpersonal relation (Kaiser & Pelphrey, 2012; Kaiser & Shiffrar, 2009; Pavlova, 2012). Social skills in ASD population may vary considerably when the IQ differences are taken into account, as the cognitive abilities can mediate the acquisition of compensatory mechanisms for dealing with social and emotional signals. For instance, some fMRI studies found a different pattern of neural activation during PLDs perception between individuals with ASD and controls, but comparable performance on behavioural task (Freitag et al., 2008; McKay et al., 2012), suggesting that observers with ASD and controls employ different neural mechanism during the visual analysis of biological motion. However, it is worth noticing that there is a lack in the literature exploring the biological motion processing in people with ASD: so far, the majority of studies has involved people with high-functioning ASD (HF ASD). Little is known about the ability of recognizing human movements and emotions in children with low functioning ASD (LF ASD), and even less is known about adults with LF ASD. Moreover,

the matching criteria commonly adopted in previous studies has been the verbal IQ, but is widely reported that non-verbal abilities are frequently higher than verbal in population with ASD. As a consequence, in previous studies the ASD groups and control groups might have not been actually matched, because the non-verbal skills were higher in participants with ASD. This might explain the absence of differences between TD and ASD reported by some previous findings (Freitag et al., 2008; Herrington et al., 2007; Murphy et al., 2009; Saygin, Cook, & Blakemore, 2010b). To avoid these kind of biases in results, in the present experiment we decided to use the non-verbal IQ as matching criteria, and to ask participants to perform a non-verbal task. The objective of our study was to explore the existence of differences between typical developing (TD) subjects and individuals with ASD in recognizing a particular aspect of biological motion: the emotional information conveyed by whole body movements. In particular we tested i) the contribution of body form and pure body motion information in the recognition of neutral and emotional actions, and ii) whether there was any difference in recognizing the bodily expression related to the emotional valence (Positive, Negative and Neutral). Additionally, we explored the relation between non-verbal IQ level, age, and the ability to recognize the meaning of human movements, measured as accuracy rate and response time. If the difficulty in ASD was related to the emotion comprehension, we expected a lower performance in recognizing emotional but not neutral movements in children with ASD – or at least in participants with high functioning ASD - with respect to TD subjects. On the contrary, if the impairment was linked to deficit in BM elaboration, ASD performance should be always lower than that of TD, independently of lighting condition and emotional content. Moreover, we hypothesised that the ability to understand BM meaning improved according to the age in TD population but not – or to a lesser extent – in ASD. Finally, we hypothesised that higher cognitive resources could i) increase the efficiency of BM

elaboration in a functioning cognitive substrate (i.e. TD), and ii) mediate the acquisition of compensatory mechanisms to obviate impairment in BM comprehension in ASD. Hence, among TD population we expected higher IQ to correlate with higher accuracy and lower RT. Besides, in ASD population, we hypothesized to find a higher accuracy rate and lower RT in HF ASD with respect to LD ASD.

1.2. Rating of the stimuli

Previous findings (Atkinson et al., 2004; Dittrich et al., 1996) showed that Point-light and Full-light displays of happy body movements can be misunderstood as angry, and fearful as sad. For this reason, prior to the effective experiment, we ran a pilot study to assess the intensity of the emotion contained in each video. Our assumption was that the clearer the portrayed movement conveys the emotion, the more “intense” the emotion would be rated. Since we are interested in exploring the ability to understand the meaning of body movement in adults and in children with ASD, we asked to rate the stimuli both to a sample of neurotypical children and to a sample of neurotypical adults. The purpose was to create an ascending order of the stimuli based on their emotional intensity, and to present the stimuli to ASD participants accordingly. The reason underpinning this choice is the following: our focus sample will include also people with LF ASD, namely people with an intelligent quotient (IQ) below 70. Notably, people with ASD – and especially LF ASD - have difficulties in focusing and in maintaining the attention, in particular when presented with social-related stimuli and tasks. In the main experiment, we will ask participants with ASD to recognize the emotional content of some body movements, thus a quite demanding task for this clinical population requiring them a strong attentional effort. Completely randomizing the order of presentation of the stimuli the most ambiguous videos could appear

consecutively in the first trials. As a consequence, ASD could disengage their attention prematurely because of the excessive difficulty of the stimuli, without being able to terminate the experiment. Therefore, to optimize the duration of ASDs' attention, we opted for presenting the stimuli according to a gradual increasing difficulty, on the basis of the emotional intensity – and thus recognisability – of the videos. To define the recognisability of each video, we run the present pilot study.

1.2.1. Participants: 21 typical developing children between 5 and 11 years old (10 females and 11 males; age M = 9.29; age SD = 1.45), and 20 neurotypical adults between 20 and 28 years old (8 females and 12 males, age M = 23.5; age SD= 2.42) participated in the pilot study. All participants had normal, or corrected-to-normal vision. Before starting the rating task, participants received an exhaustive explanation of the experimental procedure, and they were asked to read the written informative form. Informed written consent was obtained from each participant prior to the experiment, according to the Declaration of Helsinki. When participants were children, the procedure was also explained to their parents and the informed consent was signed by the both of them. The study was approved by the ethical committee of the University of Milano-Bicocca.

1.2.2. Stimuli: participants were presented with a set of digitalized video clips displaying point-light (PLDs) and full-light (FLDs) whole-body movements. The FLDs were adapted from a larger set of stimuli, originally created by Atkinson et al. (Atkinson et al., 2004) and subsequently modified by Atkinson et al. (Atkinson, Tunstall, & Dittrich, 2007). The PLDs were obtained by converting the FLDs stimuli to point-light display using Matlab (Atkinson et al., 2012) In this way, the actions represented in FLDs and in PLDs were produced from identical recordings. The FLDs consist in 3-seconds long digital movies depicting a grey-scale actor on a black background. Five females and five males between 18 and 22 years old were recruited from the final year undergraduate classes in Drama or Performing Arts at King Alfred's College

in Winchester, and were instructed to spontaneously perform emotional and neutral actions. The actors wore grey, uniform, tight-fitting clothes and a headwear, therefore the facial expression was never visible. This ensured that all the information that could be inferred from the video were conveyed uniquely from the body movement. The PLDs consisted in 2 second-long video displaying 13 white dot-lights moving on a black background. The dots were positioned over the head and over the main joints of the actor (one dot over each ankle, knee, hip, elbow, shoulder, and hand). The neutral stimuli reproduced 10 different common human movements without emotional content, and included: 1 person walking on the spot, 2 hopping, 2 digging, 1 knocking, 1 star-jumping and 3 bending to touch toes (for a total of 10 neutral PLDs and 10 neutral FLDs). The emotional actions included intended portrayal of fear, happiness, sadness or anger (the stimuli consisted in 10 different version of each of these expressions, for a total of 10 PLDs videos and 10 FLDs videos of each emotion). Examples of the stimuli can be viewed at <http://community.dur.ac.uk/a.p.atkinson/Stimuli.html>.

1.2.3. Design and procedure: All participants were tested individually in a quiet room. They were presented with a total of 40 video clips displaying point-light (PLDs) and 40 videos displaying full-light (FLDs) whole-body movements, and they were asked to rate the emotional intensity of the stimuli by using a 9-point Likert scale. Participants seated in front of an Acer notebook, with display dimension 34x19x40, located approximately at 60 centimetres from the observer. All the stimuli were presented at the centre of the screen. The experimental procedure (stimuli presentation and responses registration) was implemented with the software E-Prime 2.0[®]. Participants were asked to rate the intensity of fear, sadness, happiness, and anger. The intensity of each emotion was rated separately in four different blocks. Within each block PLDs and FLDs were presented separately, half of participants first saw the PLDs, the other half first saw the FLDs. The order of the block was counterbalanced across

participants, and within each block stimuli were presented randomly. Videos representing happy and angry movements were rated for intensity of happiness and intensity of anger; clips depicting sad and fearful actions were rated for the intensity of fear and sadness. All the videos were presented twice, in two different blocks: once they received a judgment regarding the emotion they should actually represent and once they were rated for the confounding emotion. For instance, the blocks one and two contained happy, angry and neutral videos, for a total of 60 stimuli (30 FLDs and 30 PLDs); in one block participants rated the intensity of happiness, in the other block they evaluated the intensity of anger. Similarly, the blocks three and four contain fearful, sad and neutral videos, for a total of 60 stimuli (30 FLDs and 30 PLDs); participants judged the intensity of fear and sadness separately in the two blocks. To ascertain the absence of any of the emotion the neutral videos were rated in every block. At the beginning of each block, participants were presented with the instructions. After that, a white fixation cross appeared over a black background. The appearance of the videos was activated by participants with spacebar. With children, the onset of the stimuli was activated by the experimenter. This ensured that the stimulus only appeared when participant was paying attention, and thus that the video was always entirely seen. At the offset of the video, a black slide with the question "How much ... (e.g. happy) was this person?" appeared at the top-central part of the screen and lasted until participants responded. The rating values and the associated verbal judgments were presented on the bottom of the screen. Participants were instructed to respond after the offset of the videos and to rate the stimuli by pressing the keys from "A" to "L". A sticky label over each key indicated the corresponding value from 1 to 9, with "A" corresponding to "Really not intense" and "L" to "Extremely intense".

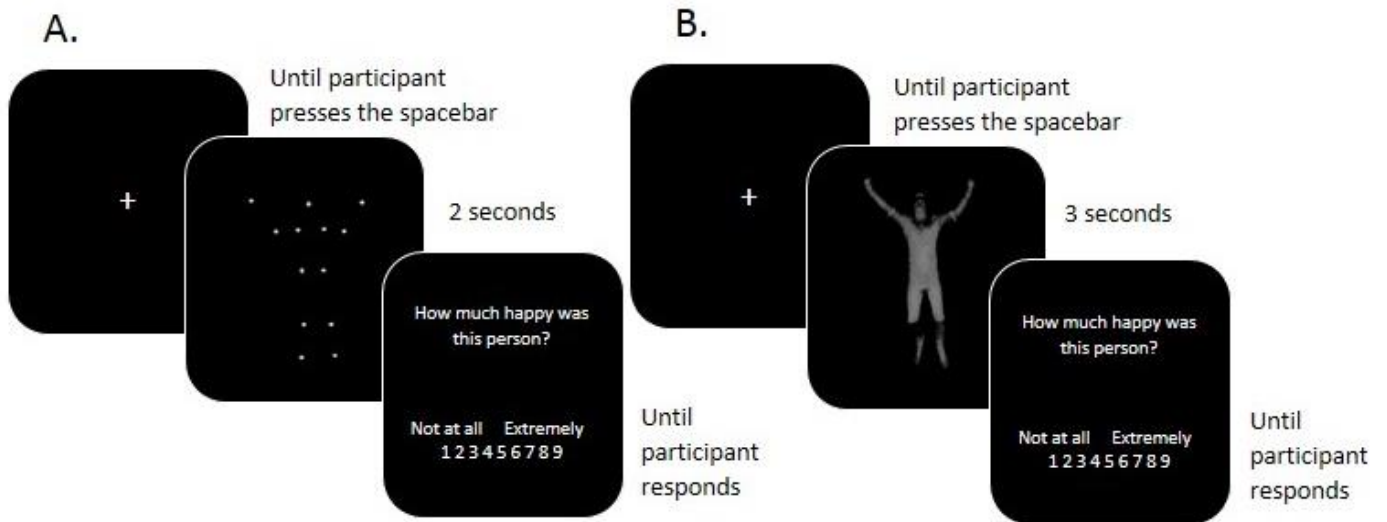


Figure 1. Rating procedure. A. Example of a PLD stimulus; B. Example of FLD stimulus.

1.2.4. Results:

The average of the scores obtained in the rating both for the actual and for the confounding emotion (i.e. video of happiness rated for intensity of happiness (actual) and for intensity of anger (confounding)) was calculated for each video. Subsequently we created an index of recognisability by subtracting the “confounding” score from the “actual” score. Finally, the order of presentation was obtained by sorting the video in ascending order according to this index.

1.3. EXPERIMENT 1: The recognition of emotional Point-Light and Full-light display in children with Autism Spectrum Disorder

To briefly resume, in the present study we were interested in understanding whether ASD difficulties were specifically related to the comprehension of the emotional content of human movements, or whether they were more generally related to the perception of biological motion. Moreover, we would

like to explore whether the ability to recognize bodily expressions improved with age. To this aim, we compared performance between children and adults. Finally, we investigated the relation between the ability to understand emotional significance of human gestures and the non-verbal IQ level.

We began our project focusing on the development of this ability, in typical and atypical population. Thus, we initially investigated the ability to recognize the emotional body language in children. In this first study we compared TD and ASD children performance when they were asked to classify the emotional valence of biological motion, depicted as short video clips of PLDs and FLDs.

1.3.1. Participants: 27 typical developing children (13 females and 14 males, age M = 8.81; age SD = 1.84; IQ M = 110; IQ SD = 14.74), 25 children with high functioning Autism (HF ASD) (1 females and 24 males, age M = 9.87; age SD = 2.9; IQ M = 100.19; IQ SD = 19.09), and 17 children with low functioning Autism (LF ASD) (2 females and 15 males, age M = 12.35; age SD = 2.11; IQ M = 44.88, IQ SD = 14.42) took part in this experiment. Two participants with LF ASD were excluded because they could not terminate the task, so a total of 15 LF ASD children were considered in the final analysis. Before starting with the experiment, all the parents received a detailed explanation of the procedure and signed the informed consent. The study was approved by the ethical committee of the University of Milano-Bicocca. Children with ASD were recruited via the Laboratory of Observation, Diagnosis and Education (ODFLab) at the University of Trento, the Autism Parents Association in Trento (A.G.S.A.T.), and the Istituto Dosso Verde in Milan. At the time of testing all participants attended normal classes at local schools and have normal or correct to normal vision. None of them had major physical disability. Including criteria: All the children with ASD met the established criteria for ASD as specified in DSM-IV (American Psychiatric Association 2006) or DSM-5 (American Psychiatric Association 2013). The

diagnosis was confirmed using the Autism Diagnostic Observation Schedule (Lord et al., 2000) and ADI and/or the ADI-R1 (Lord, Rutter, & Le Couteur, 1994). The non-verbal IQ scores were measured with the Raven’s progressive matrices (RAVEN, 1941) or the Coloured progressive matrices (John & Raven, 2003), according to participants’ age. When it was not possible to use the Raven’s Matrices because of the severity of the cognitive disabilities in participants with LF ASD, the subscales of Leiter-R brief IQ were administered (Roid GH, 1997).

Group of functioning	Chronological Age		IQ		Mental Age	
	Mean	SD	Mean	SD	Mean	SD
Children HF ASD	9.88	2.96	100.16	19.48	9.77	3.26
Children LF ASD	12.33	2.19	44.87	14.87	5.429	1.76
Children TD	8.81	1.84	110.00	14.74	9.69	2.33

Table 1. Samples’ descriptive

1.3.2. Analysis: Wilcoxon rank sum test with continuity correction was used to control that the group of TD children matched with the group of HF ASD according to chronological ($W = 297.5$, $p = .246$) and mental age ($W = 389.5$, $p = .671$), and IQ level ($W = 471$, $p = .067$). The LF ASD group was chronologically older but mentally younger both than TD (c.a. $W = 367$, $p < .001$; m.a. $W = 28$, $p < .001$) and HF ASD group (c.a. $W = 117$, $p = .025$; m.a. $W = 365$, $p < .001$). The IQ level in LF ASD was lower than HF ASD ($W = 405$, $p < .000$) and TD groups ($W = 0$, $p < .001$).

1.3.3. Stimuli: for this experiment we selected two of the four emotional categories previously rated in the pilot study (Fear and Happiness), plus the neutral movements. We selected happy and fearful expressions because they both have high arousal, but opposite valence (positive versus negative). Furthermore, from an evolutionary point of view, they have a complementary significance and generate opposite reactive behaviour: happiness signals something pleasant, something that we want to get close to and that we desire to share with other conspecifics; on the contrary fear signals a potential danger, something that we want escape from, and it is useful to distance our conspecific from the source of peril. The videos depicting emotionally neutral action were used as control stimuli. To explore whether the richness of the visual information could modulate the recognizing of the emotional valence – compared to the information conveyed by movement per se - we presented both videos of FLDs and the correspondent PLDs version. Each emotional content included 10 different movies (10 happy, 10 fearful and 10 neutral), for a total of 60 videos (30 PLDs and 30 FLDs).

1.3.4. Procedure: Participants were tested individually in a quiet room. They seated in front of a computer screen, at a distance of 60 centimetres. The experimenter seated next to the participant for the entire duration of the task. The task consisted in a dichotomous forced-choice categorization of emotional content, by keyboard. Three sticky emoticons reproducing the facial expression corresponding with the emotional valence of the body movements were placed over the response keys. Emotional categories were presented coupled in three separated blocks (Fear-Happiness; Fear-Neutral; Happiness-Neutral). At the beginning of each block, participants performed a brief practice session (consisting in 3 PLDs and 3 FLDs) to familiarize with the stimuli and with the task instructions. Each movie was preceded by a fixation cross, which lasted until the child paid attention to the monitor. At this point, the experimenter started the video. At the end of each video, participants were asked to

categorize the observed body emotion by pressing the key with the corresponding facial expression (fear, happiness, neutral). Thanks to this non-verbal procedure, we avoided to address the emotion with verbal label and we bypassed verbal instruction. Furthermore, we selected a dichotomous choice because it reduces attentional and memory resources to a minimal level. This procedure has been thought to enable also ASD with verbal disabilities and LF ASD with reduced cognitive and attentional resources to perform the task. Within each block, PLDs and FLDs were presented separately. The order of display presentation was counterbalanced across participants. Within each block the order of the stimuli was pseudo-randomized: videos were presented according to the intensity rating, but the order of the emotional category was randomized. Accuracy and response times (RTs) have been recorded.

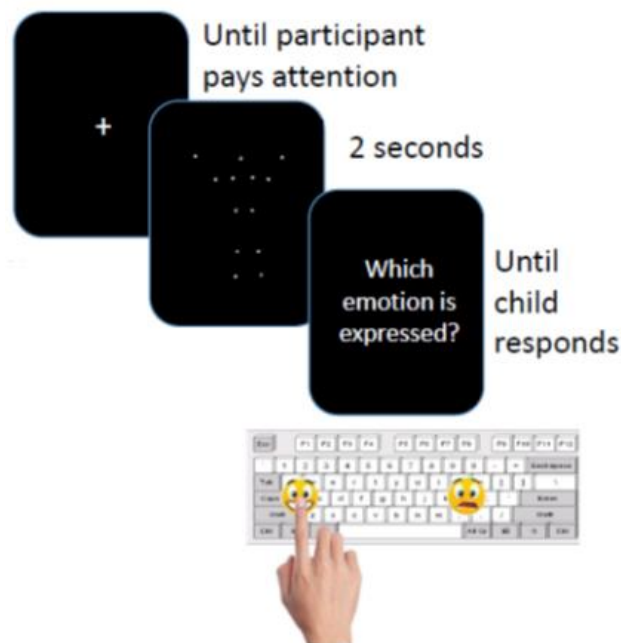


Figure 2. Procedure timeline.

1.3.5. Results: Analysis of Accuracy and response time (RTs) were performed with the R 3.3.1 package (The R core Team, 2016).

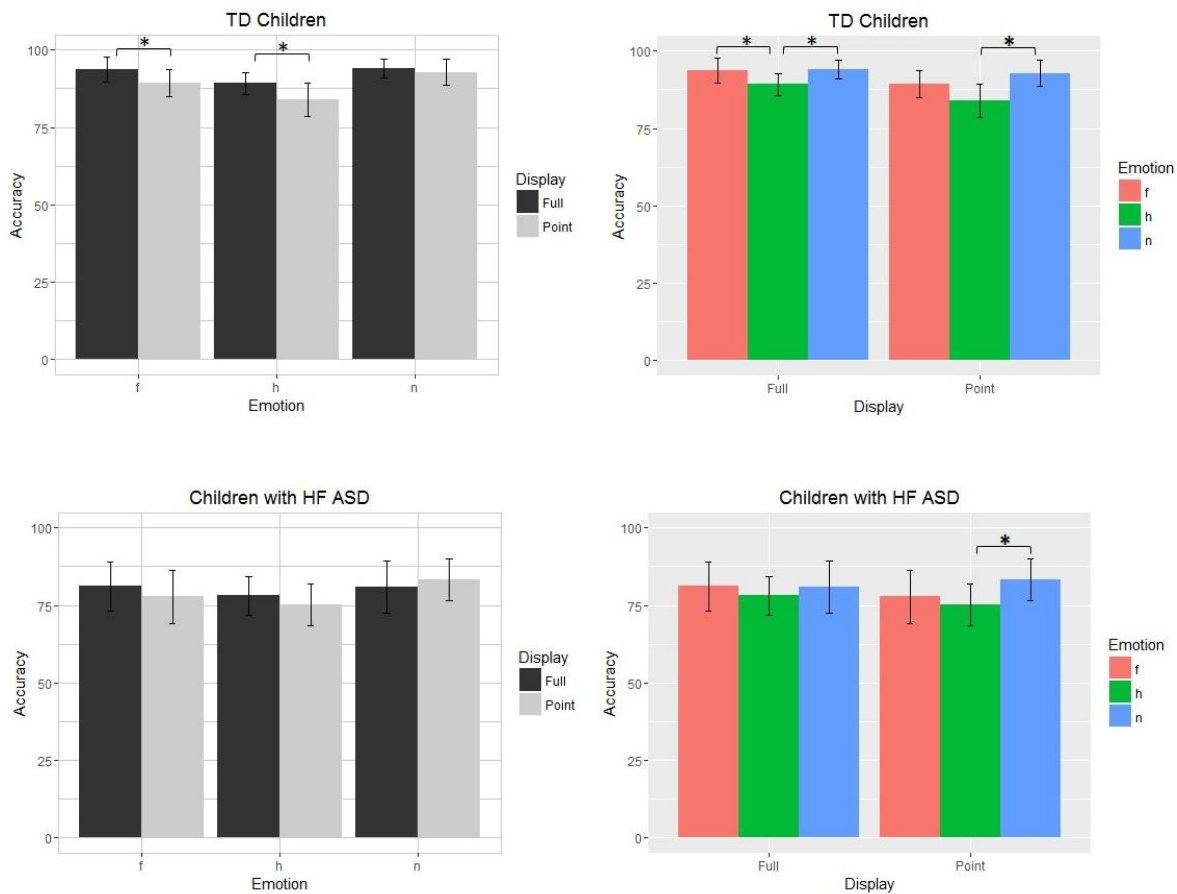
1.3.5.1. Analysis of accuracy: The percentage of the videos correctly categorised were calculated for each participant, in all the three emotional categories, both in FLDs and PLDs. To normalize the distribution of the percentage of accuracy, the arcsine square-root transformation for proportions were applied to the percentage of averaged accuracy prior to the analysis and used as dependent variable (Accuracy thereafter). We explored the differences between and within groups in recognizing i) the three emotional contents; ii) how the vision of the body form (FLDs) influenced this ability, compared to the vision of “pure motion” stimuli (PLDs); iii) the differences related to the emotional content expressed in the body movements.

Although the Accuracy relative to display and emotional category was not always normally distributed (Shapiro-Wilk normality test: children overall: $W = .94664$, $p < .001$; TD: $W = .8922$, $p < .001$; HF ASD: $W = .95138$, $p < .001$; LF ASD: $W = .97414$, $p = .069$), we decided to compute the analysis by ANOVAs because the variances were mostly homogeneous (Bartlett Test of homogeneity of variances: children overall: Bartlett's K-squared = 13.141, $df = 5$, $p = .022$; TD: Bartlett's K-squared = 4.3801, $df = 5$, $p = .496$; HF ASD: Bartlett's K-squared = 12.233, $df = 5$, $p = .032$; LF ASD: Bartlett's K-squared = 4.1629, $df = 5$, $p = .526$). In the following analysis, Display (2 levels: PLDs and FLDs) and emotion (3 levels: Fear, Happy and Neutral) were used as within variable and group of functioning (3 levels: TD, HF ASD and LF ASD) as between variable. Post hoc comparisons were permuted using pairwise t-tests and Bonferroni correction was applied to control for multiple comparisons (the p-values were multiplied for the number of comparisons and the significance level was always set at .05).

1.3.5.1.1. Within group comparison: we initially explored in each group of functioning whether the Accuracy differed between display types and emotional contents. We ran three separated 2x3 repeated measures ANOVAs, with Display and Emotion as within factors. In TD group, we found a main effects of

Display ($F_{(1,26)}= 8.14, p = .008$) and a main effect of Emotion ($F_{(2, 52)}= 5.57, p = .006$), while the interaction was not significant ($F_{(2,52)}= 2.39, p = .102$). Both the factor Display and the factor Emotion have more than one level, therefore we performed pairwise t-test (see part **1.3.5.1** for the adopted criteria) to better understand which level of the analyzed factors drove the main effects. The comparison between the levels of the factor Display showed that TD children better recognized the emotional content when conveyed by FLDs than by PLDs ($t = 2.882; df = 80, p = .005$). The comparisons between the levels of the factor Emotion revealed that in TD children happy stimuli were recognized less accurately than fearful ($p = .005$) and neutral ($p = .001$) ones, while the Accuracy did not differ between fearful and neutral stimuli ($p > .05$). The relation between the ability to recognize the emotion conveyed by dynamic body movements and the type of visual information used to represent them (pure kinematic information (PLDs) or visible body form (FLDs)) has never been explored in children so far. For this reason we considered worthwhile to explore this relation, despite the ANOVA's interaction resulted not significant. To do so, we performed post hoc comparisons between lighting conditions (Display) and Emotion. However, since the ANOVA's interaction was not significant, the results of the post hoc comparison should be interpreted just as an exploratory analysis. They revealed that in TD children happy FLDs were recognized with higher accuracy than happy PLDs ($p = .043$), and fearful FLDs marginally better than fearful PLDs ($p = .063$), while no difference was found between displays in neutral actions. With regards to the emotional content, happy stimuli seems to be harder to be identified in TD children. Indeed, happy FLDs were recognized less accurately than fearful ($p = .006$) and marginally than neutral FLDs ($p = .059$). Besides, accuracy in happy PLDs was smaller than in neutral PLDs ($p = .023$).

In both the ASD groups, results did not show any significant effect nor interaction. However, post hoc comparisons revealed that similarly to TD children, also in children with HF ASD the happy PLDs were hardly recognized than neutral PLDs ($p = .018$). No other differences were significant. Conversely, children with LF ASD seem to have more difficulties in recognizing the neutral stimuli. Indeed, accuracy was smaller in neutral FLDs than happy ($p = .018$) and marginally than fearful FLDs ($p = .078$). Finally, also in children with LF ASD the happy FLDs were recognized better than happy PLDs ($p = .038$), as it was in the other two groups.



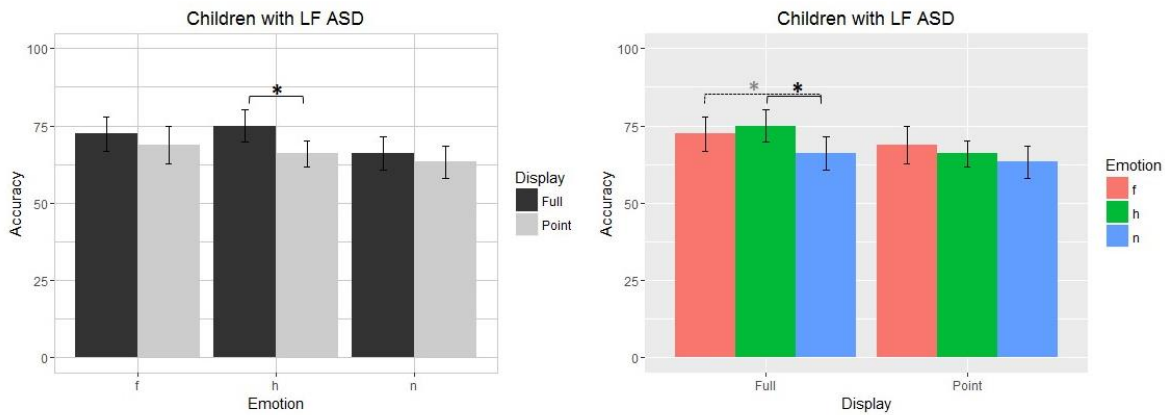


Figure 3. In the y axis is represented the Accuracy (% of correct responses/ total of items). The top row shows Accuracy in TD children, the central row shows Accuracy in children with HF ASD, the bottom row shows the Accuracy in children with LF ASD. The dark gray indicates FLDs, the light gray represent PLDs. Red, green, and blue represent Fear, Happy and Neutral respectively. The black line and black asterisks represent the significant results, the dashed line and the grey asterisk represent marginally significant results.

1.3.5.1.2. Between groups comparisons: within group analysis showed that TD and ASD processed in a different way the FLDs and the PLDs stimuli, suggesting that the visual mechanism coding for BM information works differently in the two groups. But was this processing just different or was it also less efficient? To answer this question we compared the level of Accuracy between the three groups. The averaged Accuracy for display conditions was normally distributed either for TD (Shapiro-Wilk normality test, $W = .975$, $p = .331$), HF ASD ($W = .978$, $p = .458$) and LF ASD groups ($W = .965$, $p = .419$), and variances were homogeneous (TD: Bartlett's K-squared = 1.1041, $df = 1$, $p = .293$; HF ASD: Bartlett's K-squared = .019, $df = 1$, $p = .891$; LF ASD: Bartlett's K-squared = .283, $df = 1$, $p = .594$). Therefore, a 3x3x2 repeated measures ANOVA with group of Functioning as between factor (3 levels: TD, HF ASD and LF ASD), and Display and Emotion as within factor was performed to explore whether the recognizability of the stimuli was influenced by the (i) group, (ii) the type of visual information displayed (iii) the emotional content. Results showed a significant main effect of Functioning ($F_{(2,64)} = 15.923$, $p < .001$), a

main effect of Display ($F_{(1,64)} = 10,865$, $p = .001$) and a main effect of Emotion ($F_{(2,128)} = 5.594$; $p = .005$). Also, there was a significant interaction between Display and Emotion ($F_{(2,128)} = 3.322$; $p = .039$). Post hoc comparisons showed that TD outperformed both HF ASD ($p < .000$) and LF ASD groups ($p < .001$). In turn HF ASD outperformed LF ASD ($p < .001$). Comparing the level of accuracy between displays, we found that in general FLDs were recognized more accurately than PLDs ($p < .001$). Post hoc comparison between the emotional category showed that the accuracy in happy stimuli was lower than fearful ($p = .001$) and neutral ($p = .001$). In particular, for what concerns FLDs, TD children were more accurate than both the ASD groups in recognizing fearful (compared to HF ASD ($p = .042$) and LF ASD ($p = .001$) respectively), happy (HF ASD: $p = .019$ and LF ASD: $p = .017$) and neutral stimuli (HF ASD: $p = .042$; LF ASD $p < .000$). Children with HF ASD performed better than children with LF ASD only in identifying neutral FLDs ($p = .009$). With regards to PLDs, TD's accuracy was higher than that of children with LF ASD for all the emotional contents (fear: $p = .002$; happy: $p = .006$; neutral: $p < .000$). While compared to HF ASD, TD were more accurate in recognizing neutral ($p = .029$), but not happy ($p = .086$) or fearful PLDs ($p = .118$). No differences emerged between children with HF and LF ASD.

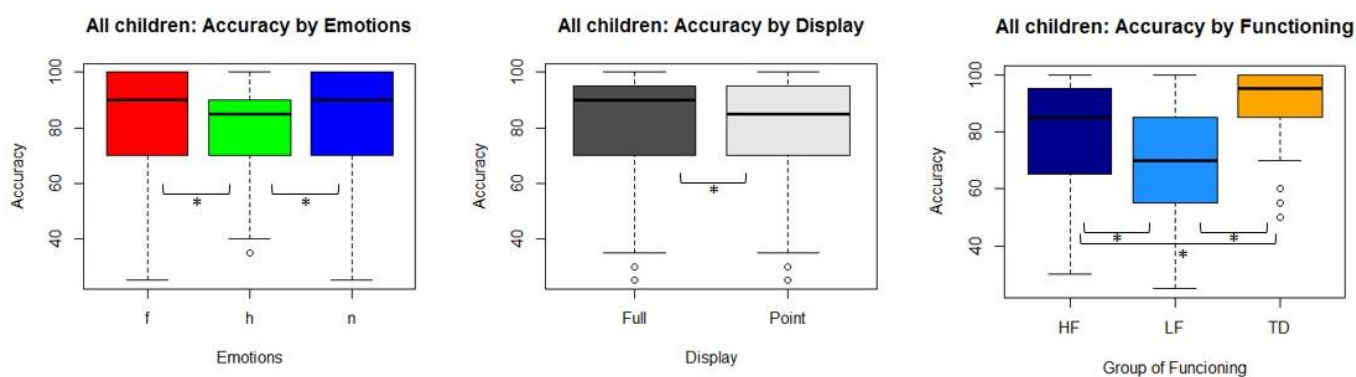


Figure 4. Significance of main effects. The black line and black asterisks represent the significant results.

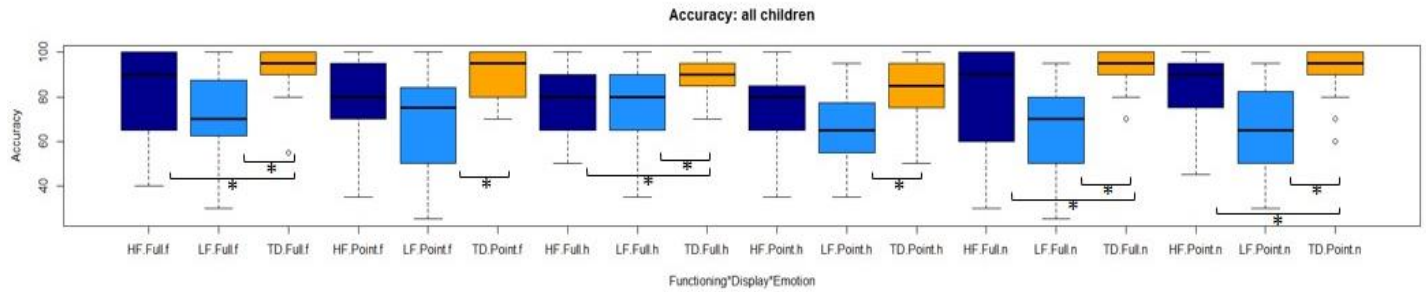


Figure 5. Significance of post hoc comparisons. Children with HF ASD, LF ASD and TD are represented in dark blue, light blue and orange respectively. Data are shown in triplets, the sequence is: Fear FLDs, Fear PLDs, Happy FLDs, Happy PLDs, Neutral FLDs, Neutral PLDs. The black line and black asterisks represent the significant results. The empty circles represent the outliers.

Since the interaction was significant, we also explored the effect of the emotion recognition separately in FLDs and PLDs. For each display condition, a 3x3 repeated measure ANOVA with Emotion as within factor and Functioning as between factor was performed.

PLD: In PLDs, results showed a main effect of Functioning ($F_{(2,64)} = 14.96, p < .001$) and a main effect of Emotion ($F_{(2, 128)} = 6.67, p < .001$). The interaction was not significant ($F_{(4, 128)} = 1.75, p = .143$). Post hoc comparisons revealed that TD were more accurate than HF ASD ($p < .001$) and LF ASD ($p < .000$), and in turn HF ASD were more accurate than LF ASD ($p < .001$). Comparison of Accuracy between the emotions showed that happy movements were recognized with lower accuracy than fearful ($p = 0.048$) and neutral actions ($p = 0.002$), while there was not difference between neutral and fearful expressions' Accuracy ($p = 0.875$).

FLDs: Results showed a main effect of Functioning ($p < .000$) and a main effect of Emotion ($p = .003$) also for Accuracy in FLDs. Post hoc comparison showed a higher Accuracy in TD with respect to both the ASD groups (all $p < .000$). HF ASD were more accurate than LF ASD ($p = 0.007$). With regards to the

main effect of Emotion, Happiness was recognized with lower accuracy than Fear ($p = 0.019$), but there was not any significant difference in Accuracy between Neutral and Happy ($p = 0.325$) or between Neutral and fearful movements ($p = 1$).

1.3.5.1.3. Relation between Accuracy, IQ and age: To explore the influence of age and IQ on the Accuracy, linear regression models were computed separately for each group. As dependent variable, the total averaged percentage of correct responses were calculated for each participant, independently of emotional content and lighting condition. To reduce the impact of deviations from normal distribution the accuracy score was arcsine transformed (Shapiro test: $W = .970$, $p = .1087$) before computing the analysis. Results of the linear model in TD group showed that the age only marginally predict the Accuracy ($F_{(1,25)} = 3.308$; $p=0.081$; $R^2 = 0.117$; adjusted $R^2 = 0.081$) while the IQ level do not contribute to determine the performance, suggesting that in TD children the IQ is not related to the ability of recognizing emotional body expressions. According to a backward stepwise regression (based on the selection of the model with the minimum Akaike Information Criterion – AIC), the best model to explain Accuracy in children with HF ASD was the multiple regression with IQ and age as factor, without interaction ($F_{(2,22)} = 6.768$, $p = .005$; $R^2 = 0.38$; adjusted $R^2 = 0.325$). This model showed that the ability to correctly recognize the emotional valence of whole body movement in HF ASD children was predicted by both the IQ level ($t = 2.31$, $p = 0.029$) and the age ($t = 3.290$; $p = 0.003$). Finally, also in LF ASD group the model for explaining the Accuracy includes the IQ and the age without interaction. However, the overall model is not significant ($F_{(2,12)} = .123$; $p = .123$; $R^2 = 0.179$; adjusted $R^2 = 0.111$) and it showed that the age did not ($t = 1.858$; $p = .113$) and the IQ did only marginally ($t = 1.349$; $p = .073$) predict the Accuracy. Thus, neither the age nor the IQ influenced the ability to recognize emotional body motion in LF ASD.

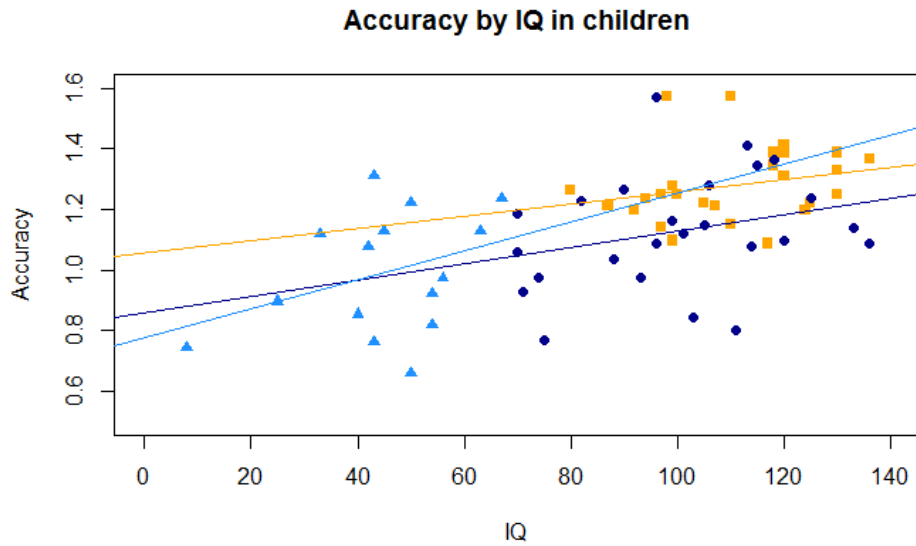


Figure 6. Relation between Accuracy and IQ in the three groups of children. Children with HF ASD, LF ASD and TD are represented in dark blue (circles), light blue (triangles) and orange (squares) respectively.

1.3.5.2. Analysis of response times (RTs)

Group of functioning	RT msec	RT log	Chronological Age		IQ		Mental Age	
			Mean	SD	Mean	SD	Mean	SD
Children HF ASD	2446.09	0.89	9.88	2.96	100.16	19.48	9.77	3.26
Children LF ASD	2488.12	0.911	12.33	2.19	44.87	14.87	5.43	1.76
Children TD	1437.19	0.363	8.81	1.84	110.00	14.74	9.69	2.33

Table 2. Descriptive and vital statistics in children.

For the analysis of RTs only the correct responses were considered. For each participant, we discharged the RTs outliers, calculated according to the following formula:

$$Q_3 + 3*(Q_3 - Q_1) < RT < Q_1 - 3*(Q_3 - Q_1)$$

Where Q_1 indicate the 1° quartile, and Q_3 indicate the 3° quartile. This formula is more frequently adopted multiplying the interquartile difference by 1.5 instead of 3. But since the error rate was high in LF ASD group, we preferred to use a less conservative calculation in order to keep a good number of observation in each cell and thus obtaining more meaningful results in the analysis. According to these criteria, a total of 22.82% of trials were discarded from the analysis (specifically 12.26% of trials in TD group, 25.91% in HF ASD and 36.76% in LF ASD). To reduce the deviance from the normal distribution the rough RT were transformed using natural logarithms. This measure was used as dependent variable (logRT hereafter). In every group we calculated the mean of logRT relative to display conditions and emotions. Data distribution was controlled with Shapiro tests and homoscedasticity of variances was controlled with Bartlett test. Similarly to analysis of Accuracy, also in the ANOVAs with RTs Emotion (Fear, Happiness, Neutral) and Display (FLDs and PLDs) were used as between factors, and group of functioning (TD, HF ASD, LF ASD) as between factor. Post-hoc comparisons were permuted with pairwise t-test and Bonferroni correction was used to adjust for multiple comparisons.

1.3.5.2.1. Within group analysis: as we did for analysis of Accuracy, we initially analysed the RTs within group to explore the presence of differences between Display and Emotion. A 2 (display) x3 (emotion) repeated measures ANOVA was performed separately in each group of functioning. In **TD children**, results showed a **main effect of Emotion** ($F_{(2, 52)} = 3.83$, $p = 0.028$), **but no differences in RTs between Display**. As we did for the analysis of the Accuracy, we compared the levels of the factor Emotion to understand which of them drove the main effect. Results in TD children revealed that, overall, **fearful** videos were recognized **faster** than **happy** ($p = .002$), but no other differences were found between happy and neutral, or fearful and neutral stimuli. Similarly to analysis of Accuracy, we investigated the relation between the rapidity in recognizing the bodily emotions and their visual representation,

although the ANOVA's interaction was not significant. For this reason, those results should be interpreted just as an exploratory analysis, as we recommended above (part **1.3.5.1.1.**). To this aim, we performed post hoc comparison of the emotional content across displays, showing that **fearful FLDs** were recognized **faster** than **fearful PLDs** ($p = .018$). No other comparison was significant. Result in children with **HF ASD** did not show **any significant effect or interaction**. Finally, results in children with **LF ASD** showed a significant effect of Emotion ($F_{(2,28)} = 3.97$, $p = .030$) – similarly to TD children - with **fearful stimuli recognized faster than happy** ($p = .028$) and neutral ones ($p = .050$). Post hoc comparisons did not show any significant difference neither in children with HF ASD nor in children with LF ASD.

1.3.5.2.2. Between groups analysis: as it was for analysis of Accuracy, within group results suggest that the three groups elaborate the body stimuli differently. To understand whether this different processing was also less efficient, we compared the rapidity in recognizing the bodily expressions between the three groups of children. To this aim, a $2 \times 3 \times 3$ repeated measures ANOVA with Emotion and Display as within variables and group of functioning as between factor was computed. Results showed a main effect of Emotion ($F_{(2, 128)} = 6.956$, $p = .001$), a marginally significant effect of Display ($F_{(1, 64)} = 3.80$, $p = .056$), but the **effect of Functioning** was **not significant** ($F_{(2,64)} = 1.255$, $p = .292$). Furthermore, the interaction between functioning and display was marginally not significant ($F_{(2,64)} = 2.631$, $p = .079$), while the other interactions were not significant at all (all $p > .3$). These data suggest that **the time needed for recognizing the body motion is just marginally modified by the vision of body shape relative to the vision of pure motion information**. The absence of significance for the effect of Functioning suggests that children with **ASD and TD children recognize the emotional meaning of the body movement with the same rapidity**. Post hoc comparisons of emotional contents showed that, in general, fearful stimuli were recognized faster than happy ($p < .001$) and neutral items ($p = .004$), while

no difference emerged between happy and neutral stimuli ($p > .05$). Moreover, despite no significant main effect of Functioning, post hoc comparisons showed that, overall, TD children were faster than children with HF ASD ($p = .003$) and LF ASD ($p = .017$), while no difference was found between the two groups of children with ASD. However, this difference was present only when RTs were considered overall. Indeed, when the RTs were specifically compared in every condition, no group differences emerged, neither in FDLs nor in PLDs, in any of the emotional content, confirming the absence of a significant main effect. Finally, the marginal effect of the interaction between Display and Functioning was explained by the fact that TD resulted faster than HF ASD ($p = .011$) and LF ASD ($p = .014$) in recognizing PLDs stimuli, but there was not any group difference between RTs in FDLs (all $p > .2$).

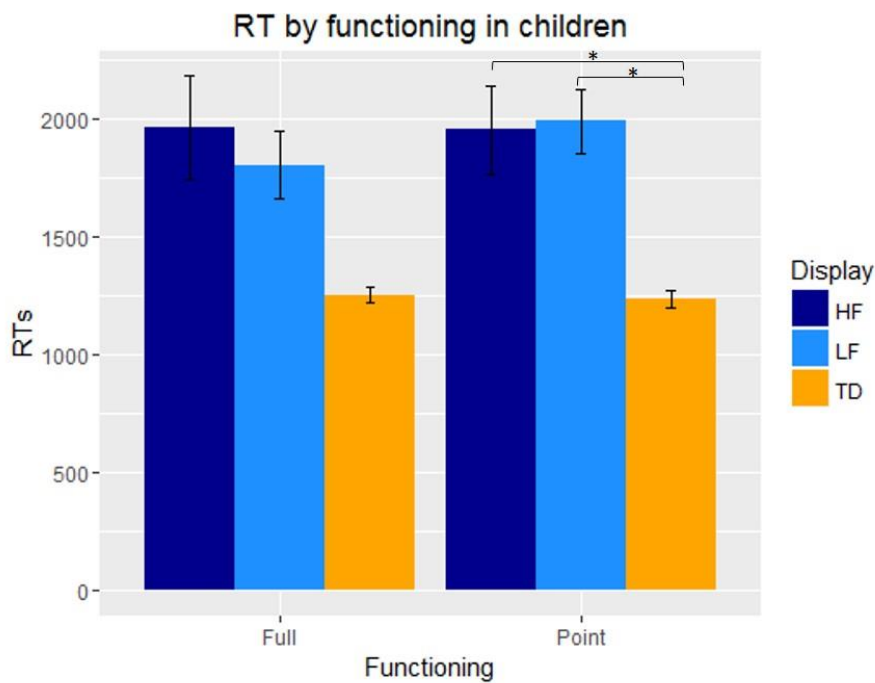


Figure 7. Representation of the interaction between Display and Functioning. The graph shows RTs as means; children with HF ASD, LF ASD and TD are represented in dark blue, light blue and orange respectively. Significant results are represented with square brackets and asterisk.

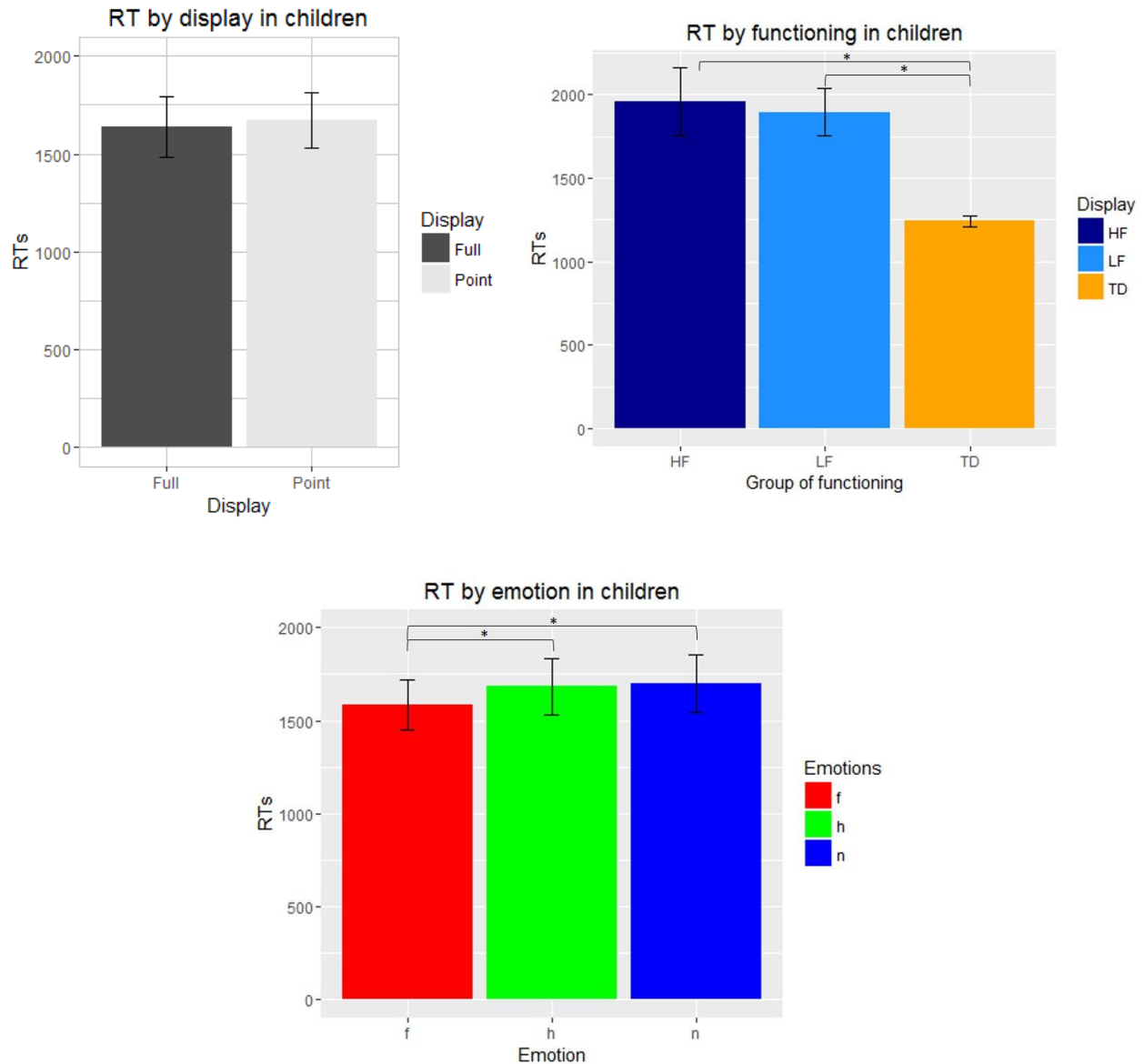
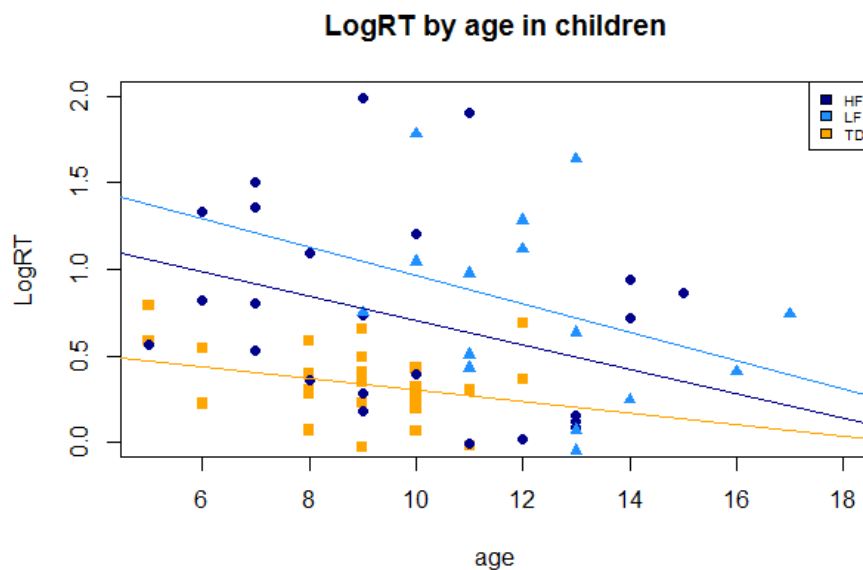


Figure 8. The three graphs represent the ANOVA's main effects. The first graph shows the effect of Display; the second graph show the effect of Functioning; the third graph represents the effect of Emotion, which was the only being significant. Fear is represented in red, Happiness in green and Neutral in blue. Significant results of post hoc comparisons are represented with square brackets and asterisk. The vertical black bars represent standard errors.

1.3.5.2.3. Relation between RT, IQ and age: To explore whether the response time change according to IQ and age, we computed linear regression model separately for each group. A stepwise regression analysis and anova comparison of the models were used to determine which model better explained

the relation between the considered factors. In **TD group**, the best model to explain RTs was the one considering both IQ and age, with no interaction. Results of this linear model ($F_{(2, 159)} = 7.87$, $p < .001$, $R^2 = .090$, adjusted $R^2 = .079$) showed that **only the IQ was a significant predictor of the RTs** ($t = -3.715$; $p < .001$). In the **HF ASD** group, the best model was the one considering the IQ and the age in interaction ($F_{(3,146)} = 9.735$, $p < .000$; $R^2 = .167$; adjusted $R^2 = .149$). Results of this model showed that **both the IQ** ($t = 2.4$; $p = .018$) **and the age** ($t = 2.768$; $p = .006$) predicted the RTs **and the interaction** was also significant ($t = -3.443$; $p = 0.001$). Finally, also for the **LF ASD** group the best model to explain the RTs was considering IQ and age in interaction ($F_{(3,86)} = 40.66$, $p < .000$; $R^2 = .586$; adjusted $R^2 = .572$). This model showed a **significant interaction between age and IQ** ($t = -2.761$; $p = .007$), but the effect of IQ itself was not significant and the effect of age was marginally not significant ($t = 1.101$; $p = .072$).



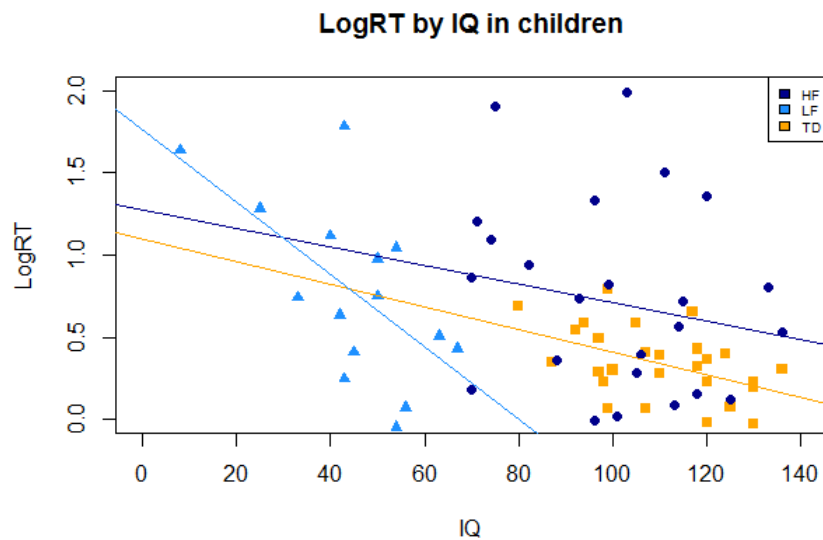


Figure 9. Linear regression of LogRT and age (top graph) and LogRT and IQ (bottom graph) in the groups of children. The dark blue line and circles indicate the HF ASD, the light blue line and triangles indicate the LF ASD, the orange line and squares indicate the TD.

1.3.6. Discussion

In this first study, we compared the ability of recognizing neutral and emotional body language between TD children and children with ASD with different levels of functioning. The aim of our study was i) to investigate whether the difficulties in ASD population were associated to emotion comprehension or related to a more basic visual processing of biological motion, and ii) to explore whether this ability improved according to the age and to the non-verbal IQ. To this purposes, we presented point-light (PLDs) and full-light (FLDs) version of human movements with three different emotional valences (Happy, Fearful, Neutral). Our results showed that TD children were more accurate than children with ASD in recognizing the emotional valence of BM. Also, children with HF ASD outperformed children with LF ASD. However, we did not find group differences in RTs. Our results are in line with previous findings (Annaz et al., 2010; Blake, Turner, Smoski, Pozdol, & Stone, 2003; Hubert et al., 2007; Moore et al.,

1997; Parron et al., 2008), and confirm that children with ASD have difficulties in comprehending the meaning of body movements. Furthermore, our data suggest that when the emotional valence is correctly understood, the time needed to process the emotional content of body movement is similar in TD children and children with ASD.

1.3.6.1. Differences between Full-light and Point-light display of body movements

The majority of previous researches explored the comprehension of biological motion in ASD using PLDs. However, in the real world the body form is fully shaped and this should be taken into account when difficulties in social interaction are investigated. Therefore, besides PLDs we asked participants to recognize FLDs. To avoid possible confounds related to differences in the quality of the movement between the two display conditions, we used stimuli containing identical quality and intensity of movement, as the PLDs were created converting the FLDs footages (Atkinson et al., 2004, 2007, 2012). In line with previous findings in adults (Atkinson et al., 2004; Ross, Polson, & Grosbras, 2012), we found that TD children were more accurate in recognizing the emotional content of body movements when the shape of the body was visible (i.e. FLDs), compared to the view of pure motion information (i.e. PLDs). Therefore, our findings demonstrate that TD school-aged children are able to correctly identify the emotional valence of dynamic bodily expression, also when the form information is minimized by presenting PLDs. However, there was just a marginal difference in RTs across the display conditions. Those results showed that in TD children the vision of body form facilitates the recognition of the emotional content, and it partially speeds the identification of bodily expressions. With regards to ASD, we initially hypothesized that if the deficit in understanding social signals in individuals with ASD was due to an impairment in BM elaboration, this deficit should be independent of display condition and consistent across the emotional contents. According to this assumption, our results showed that

children with ASD - irrespectively to their IQ level – did not benefit from the richness of visual information, and that their ability to recognize BM did not change according to the emotional valence. In fact, compared to TD children, children with ASD were impaired not only in understanding the emotional expressions, but also in recognizing the neutral actions. This finding suggests that the difficulty encountered by individuals with ASD in social interaction could be more generally related to the biological motion elaboration, rather than being specific for the emotions comprehension. This hypothesis is supported by the fact that despite the two types of display contain exactly the same quantity and quality of movement (PLDs clips were created converting the FLDs ones), the richness of visual information did not facilitate the elaboration of BM in ASD - as it did for TD children. Hence, the lack in emotion recognition in ASD seems to be attributable to a deficit in elaborating the motion cues rather than the emotional information.

1.3.6.2. Differences across emotional contents

According to the emotional content, we found that the valence had an effect on the performance of TD children. In previous findings, happiness has sometimes been reported as the emotion most easily recognized in children (de Meijer, 1989; Lagerlöf & Djerf, 2009). However, Ross and collaborators (Ross et al., 2012) did not observe any advantage for happiness, and other studies have reported advantages in recognizing fear using images of emotional body (Atkinson et al., 2004; Bannerman, Milders, de Gelder, & Sahraie, 2009). In line with those latter evidences, our data showed that TD children recognized happy bodily expressions with lower accuracy than fearful and neutral movements. Besides, fearful movements were identified more rapidly. We interpreted these results as following. From an evolutionary point of view, the reason why emotional expression has developed was to signal something. In particular, the purpose of fear is to signal a potential source of danger, something that is

advisable to stay away from. The vision of someone expressing fear lets us suppose that there is something scaring close to him/her. According to that, it is more important to recognize fearful expression when the agent is far from us, as the larger is the distance between us and the scaring object, the greater is the time we have for getting away safely. Conversely, happiness serves as a signal for something pleasant that we potentially would like to get close to and to share. Indeed, smiling is a valuable mechanism for forming and maintaining cooperative relationships. Hence, evolutionary speaking, it is much more functional to recognize happiness when the agent is close to us, because the proximity to the positive stimulus allows the observer to reach it easily. When we are close to another person, face is the favourite channel we usually attend for understanding the emotions. But when the agent is distant, the face could not be visible anymore and thus the main informative channel for inferring others' feeling and intentions becomes the body. In our experiment we used stimuli depicting body movement, thus it is not surprising that fear was the emotion recognized faster and that happy movements were more arduous to be disentangled.

1.3.6.3. Relation between IQ, age and the recognition of body language

Regarding the relation between IQ level and BM recognition, in this experiment we decided to use the non-verbal abilities as matching criteria because we hypothesised that non-verbal competences - more than verbal ones - might reflect the general efficiency of the cognitive substrate. The non-verbal abilities correspond with the fluid intelligence - namely the ability to reasoning, to find new solution and to solve problems - that is innate and not acquired. It is possible, although speculative, that in children with ASD, higher cognitive resources underlie the developing of alternative strategies to compensate the difficulties encountered in recognizing the bodily expressions. Besides, we were interested in exploring differences in the developmental trajectory of BM elaboration between TD children and children with

ASD. Our results showed that in TD children the Accuracy in recognizing the emotional valence of whole body movements was marginally predicted by the age but not by IQ, suggesting that when the mechanism that codes for the emotional body movement is functionally integer – as it is in TD children – the ability to recognize the bodily expression improves with age. This is in line with previous findings, showing that the progressive neural maturation occurring with age corresponds with an improvement of BM processing (Hirai, Watanabe, Honda, & Kakigi, 2013; Robbins & Coltheart, 2015; Ross et al., 2012). Furthermore, in TD children the IQ level did not predict the Accuracy, suggesting that when the mechanism for the BM elaboration works properly, its functioning is independent from the general cognitive resources. Contrarily to the Accuracy, in TD children the RTs were predicted by the non-verbal IQ. This suggests that a higher level of cognitive resources increases not the efficacy but the efficiency of the mechanism underling the comprehension of body expression, reflected in a more rapid elaboration of the emotional content of body movements. For what concerns results in ASD groups, we found that in children with HF ASD both the Accuracy and the RTs were predicted by the interaction between age and IQ. In children with LF ASD neither the IQ nor the age modulated the Accuracy, but the RTs were predicted by the interaction between age and IQ. These findings suggest that when the mechanism for the BM processing is impaired – as it is in children with ASD (Annaz et al., 2010, 2012; Blake et al., 2003; Freitag et al., 2008; Hubert et al., 2007; Kaiser & Pelphrey, 2012; Moore et al., 1997; Parron et al., 2008; Philip et al., 2010) – a more efficient cognitive substrate might subtend the acquisition of compensatory mechanisms and strategies to understand bodily expressions, that seems to improve with age. Presumably, these strategies are sophisticated and require considerable cognitive efforts and herefore they can developed only in presence of high IQ level. Furthermore, those alternative strategies likely become more and more efficient with the practice, i.e. with age. According

to these premises, we found that the Accuracy was related to IQ and age only in children with HF ASD. In fact, children with LF ASD the ability to recognize the meaning of body movements was greatly impaired but it was not predicted by the IQ level, suggesting that when the cognitive resources are low it is harder to develop compensatory mechanisms. However, our results showed that the efficiency of spared abilities improve with age and IQ in children LF ASD. This means than even though the difficulties of children with LF ASD in understanding the emotional meaning of body movement remain stable during the development, when they are successful in comprehending the BM they do it more rapidly. Previous studies using full scale IQ score as matching criteria between TD and ASD children (Parron et al., 2008) failed to find a significant relation between IQ and the ability to recognize the emotion from PLDs. On the contrary, we found clear group difference using the non-verbal IQ. Hence, the non-verbal IQ seems to be a more adapt measure of cognitive abilities in participants with ASD and using it as matching criteria with the control group reduces criticalities related to uneven cognitive profile in ASD population, and allows to detect group difference in recognizing the messages conveyed by the body.

1.4. EXPERIMENT 2: How do adults with ASD recognize the emotional body language?

1.4.1. Introduction

It is interesting to note that studies involving children with ASD and TD controls tend to find significant differences between the groups (e.g. Blake et al., 2003 Ages 8–10; Klin, et al., 2003 Aged 2; Klin, et al., 2009 Aged 2; Annaz et al., 2010 Ages 5–12). On the contrary, studies using adults tend to find no differences (e.g. Hubert, et al., 2007 Ages 15–34; Murphy, et al., 2009 Mean Age 26; Atkinson, 2009 Ages 18–58) and those that use an intermediate age range tend to find mixed results (e.g. Moore, et al., 1997 Ages 11–19; Parron, et al., 2008 Ages 7–18). This research suggests that there may be a

dysfunction in biological motion processing amongst people with ASDs, that is still clearly evident at a young age, but that may be hidden by compensatory mechanisms later in life. These mechanisms may be due to adults with ASDs accomplishing the same tasks using different brain regions and pathways, which have adapted to compensate these functions. Evidences from neuroimaging seems to corroborate this hypothesis. Autistic individuals exhibited reduced fMRI response to PLDs in right superior temporal sulcus and Fusiform gyrus (Kaiser et al., 2010). A series of fMRI studies found comparable behavioural performance, but distinct neural activation between ASD and TD groups in biological motion processing. For example, asking adolescents with ASD to recognize neutral PLDs from scrambled PLDs, Freitag and collaborators (Freitag et al., 2008) found no difference in error rate but increased RTs with respect to TD controls . Also, the authors found strong group differences in neural activation during passive view biological motion perception, in particular hypoactivation of the inferior parietal lobules (IPL) and middle temporal gyrus (MTG) in the right hemisphere, and the fusiform gyrus (FFG) and superior temporal gyrus (STG) in the left hemisphere. Individuals with ASD showed a sparse activation of brain region and no difference between biological and non-biological stimuli in the superior temporal sulcus (pSTS). Likewise, in another study, Herrington et al (Herrington et al., 2007) found different patterns of neural activation to PLDs versus fixation in STS, IPL, and FFG. McKay and collaborators (McKay et al., 2012) reported different connectivity between areas coding for the biological motion, suggesting that to achieve TD-comparable levels of BM processing individuals with ASD recruit independent cortical network.

In our first experiment we have inquired the ability in recognizing the emotional valence of Point-light and Full-light display of human body movement in children with ASD and typically developing. In line with previous findings, our results confirm an impairment in understanding the BM in children with

ASD. In addition to that, our findings revealed that the difficulties in ASD were not specific for the recognition of the emotions, but they extended also to the comprehension of neutral action. Moreover, we found that this impairment was present independently whether the body shape or only the motion information were visible. This suggest that children with ASD might use different mechanisms for recognizing the body expressions, which are less effective and less efficient. To interpret the body movements they may adopt compensatory mechanisms, which acquisition seems to be mediated by the non-verbal IQ and improving with age. If this was the case, we should expect an improvement in the ability of recognizing the BM in adults with ASD, with respect to children with ASD, and this improvement should have been correlated with the non-verbal IQ level. To explore this hypothesis, we run a second experiment, where we asked to a group of TD adults, a group of adults with high functioning Autism matched for age and non-verbal IQ, and a group of adults with low functioning Autism matched for age, to performed the same BM recognition task that children did in our first experiment.

1.4.2. Participants: a total of 30 neurotypical adults (15 females and 15 males, age M = 25.1, age SD = 5.43; IQ M = 119.1 , IQ SD = 10.75), 15 adults with high functioning Autism (1 female and 14 males, age M = 23.6, age SD = 6.67 ; IQ M = 110, 93, IQ SD = 15.12) and 10 adults with low functioning Autism (2 females and 8 males, age M = 23.57, age SD = 5.32; IQ M = 47.86; IQ SD = 18.60) participated in this experiment. Two LF ASD could not terminate the task, for this reason they have been excluded from the analysis.

Group of functioning	IQ		Age	
	Mean	SD	Mean	SD
Adult TD	119.10	10.75	25.10	5.43
Adult ASD LF	47.86	18.60	23.57	5.31
Adult ASD HF	110.93	15.12	23.60	6.67

Table 3. Descriptive and vital statistics in adults.

All participants had normal or correct to normal vision. Before the experiment, all participants or their legal ward received a detailed explanation of the procedure and signed the informed consent. The study was approved by the ethical committee of the University of Milano-Bicocca. Participants with ASD were recruited via the Laboratory of Observation, Diagnosis and Education (ODFLab) at the University of Trento, and the Autism Parents Association in Trento (A.G.S.A.T.). At the time of testing none of participants had major physical disability.

Including criteria: All participants with ASD met established criteria for ASD as specified in DSM-IV (American Psychiatric Association 2006) or DSM-5 (American Psychiatric Association 2013). The diagnosis was confirmed using the Autism Diagnostic Observation Schedule (Lord et al. 2000) and ADI and/or the ADI-R1 (Lord, Rutter, & Le Couteur, 1994). Non-verbal IQ scores were measured with the Raven's progressive matrices (Raven 1936) or the Coloured progressive matrices. Wilcoxon rank sum test with continuity correction was used to control for IQ and age matching between groups. The group of TD was IQ-matched with the group of HF ASD ($W = 284.5$, $p = 0.061$), and age-matched with both HF and LF ASD groups ($W = 279$, $p = 0.081$; $W = 124.5$, $p = 0.455$, respectively). Also the two ASD groups were age-matched ($W = 49.5$, $p = 1$).

1.4.3. Procedure: In this Experiment 2, to test the ability in recognizing the valence of body expression in adults we used the same procedure that we adopted with children. A detailed explanation could be found in the paragraph “Procedure” of the Experiment 1.

1.4.4. Results

1.4.4.1. Analysis of Accuracy: as in Experiment 1, the accuracy was averaged by emotion and display condition for every participant and the arcsine transformation of those values was used as dependent variable (Accuracy). Emotion (Fear, Happiness and Neutral) and Display (FLDs and PLDs) were used as within factors, and group of functioning (TD, HF ASD, LF ASD) as between factor.

1.4.4.1.2. Within group analysis: we were initially interested in exploring differences in Accuracy between display condition and emotions within group. To this purpose, a 2x3 repeated measures ANOVA with Display and Emotion as within factors was performed independently in each group. In **TD** adults, we found a significant main effect of Display ($F_{(1,29)} = 5.817$, $p = .022$) with **FLDs** recognized **better** than **PLDs** ($p = .013$), and a significant main effect of Emotion ($F_{(1,58)} = 8.070$, $p = .001$), with **Happiness** recognized with **lower** accuracy than **Fear** ($p < .001$) and Neutral ($p = .003$). In particular, post hoc comparison in FLDs showed that accuracy was significantly lower in happy than fearful videos, and in PLDs happy was lower than fearful and neutral stimuli. In **ASD** groups we did not find **any significant effect of interaction**. This results suggest that the ability of recognising the body expressions in **ASD** adults was not modulated neither by the type of visual information nor by the valence of the emotion conveyed by the body movements. **They did not seem to benefit from the view of the body form, the richness of the visual information is not helpful for them.**

Within analysis showed that the performance of ASD group was qualitative different from TD's one, but was it equally accurate? Were individual with ASD impaired in recognize the emotional valence of body language with respect to TD? To answer this issues we compare the Accuracy between groups.

1.4.4.1.3. Between group comparison: A 2x3x3 repeated measures ANOVA with Display and Emotion as within factor and Functioning as between factors was performed to explore whether there was any difference in Accuracy between the three groups according to display condition and emotion. Results showed a **main effect of Functioning** ($F_{(2,49)} = 54.66, p < .001$), a main effect of Emotion ($F_{(2,98)} = 3.51, p = .033$) and a main effect of Display ($F_{(1,49)} = 8.62, p = .005$). Overall, i) **TD adults outperformed participants with HF and LF ASD** (both $p < .001$) and **HF ASD were more accurate than LF ASD** ($p = .004$); ii) FLDs were recognized better than PLDs ($p = .001$); iii) Accuracy in happy stimuli was significantly lower than fearful ($p = .007$) and neutral videos ($p = .004$). In particular, post hoc comparisons revealed that adults with LF ASD were less accurate than TD and HF ASD (both $p < .001$) in recognizing FLDs and PLDs (all $p < .001$), while the difference between adults with HF ASD and TD was not significant in PLDs ($p = .093$) and marginally not significant in FLDs ($p = .052$). Comparing the Accuracy between the emotional contents, we found that LF ASD were significant less accurate than TD and HF ASD in identifying all the emotional content (all $p < .001$), while adults with HF ASD performed worse than TD in fearful ($p = .035$) and neutral stimuli, but in this latter the result was no more significant when Bonferroni adjusted ($p = .072$).

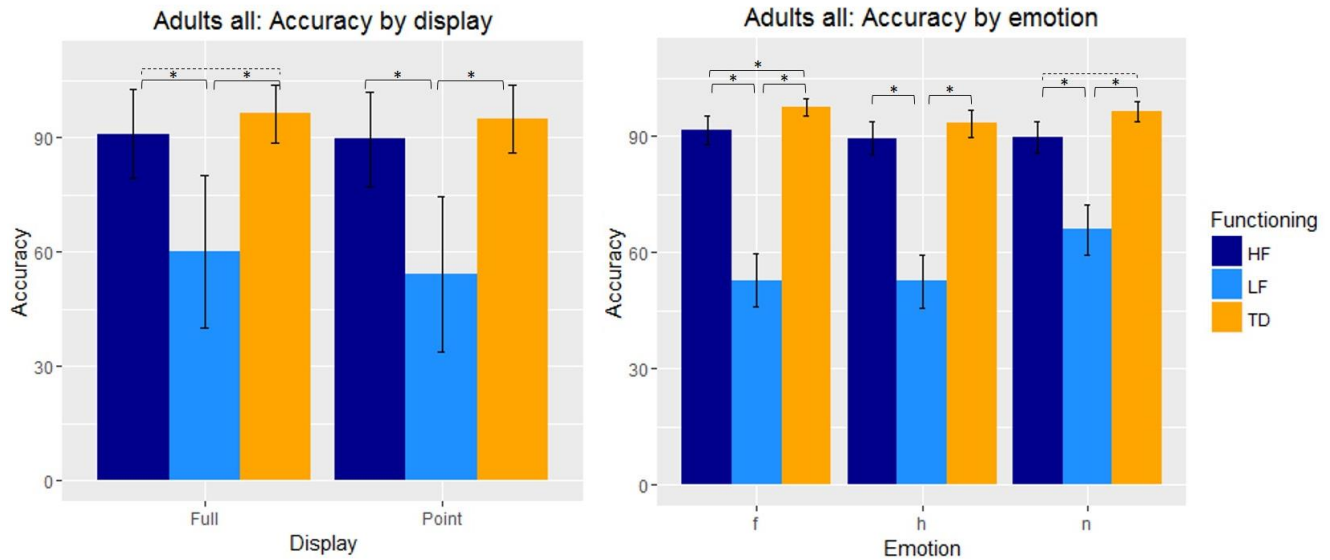


Figure 10. Representation of differences between groups of adult participants in Accuracy among Displays (left graph) and Emotions (right graph). In this latter, the x axis shows the three emotional valence: f is for Fear, h is for happiness, n is for neutral. Significant results of post hoc comparisons are represented with square brackets and asterisk, dashed lines represent marginally significant results. The vertical black bars represent standard errors.

1.4.4.1.4. Regression model with IQ and accuracy: Three different linear models were created to explore the relation between IQ and Accuracy separately in each group. Result showed that the non-verbal **IQ significantly** predicted the ability to recognize the meaning of BM **in TD** ($F_{(1,28)}: 6.283, p = .018; R^2 = .183; \text{adjusted } R^2 = .165$) **and** in individuals with **HF ASD** ($F_{(1,13)}: 12.81, p = .003; R^2 = .496 ; \text{adjusted } R^2 = 0.457$), **but not in LF ASD**. Specifically, the relation was positive: this means that lower non-verbal IQ levels corresponded with higher Accuracy.

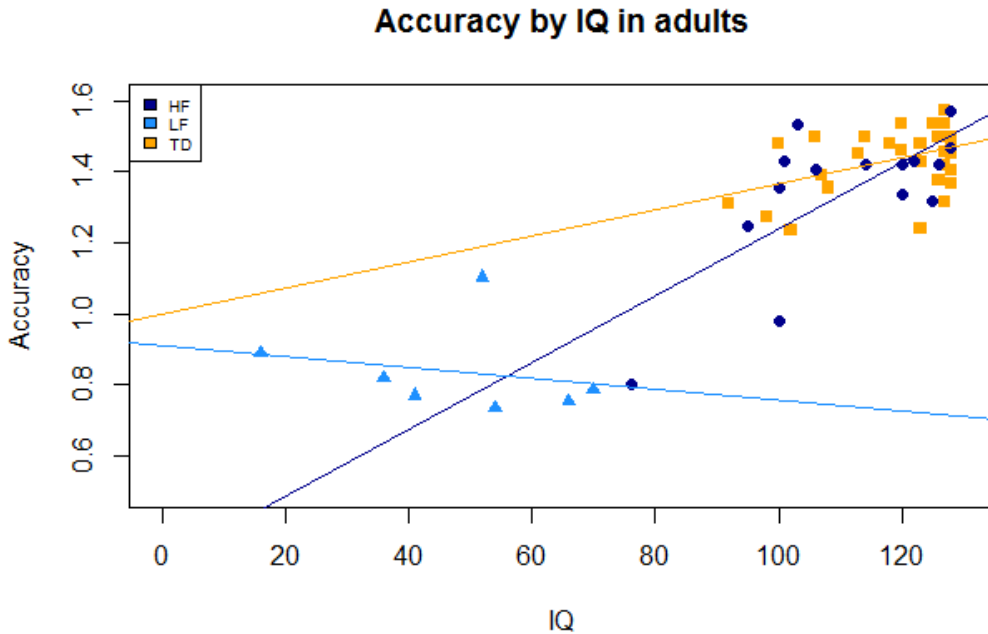


Figure 11. Linear regression between Accuracy and IQ in adults. The dark blue line and circles indicate HF ASD, the light-blue line and triangles indicate LF ASD, the orange line and squares indicate TD.

1.4.4.2. Analysis of response times (RTs): Only the response time relative to correct responses has been considered in the analysis. A total percentage of 13.41% of incorrect responses has been discharged, subdivided as 10.40% of responses in TD group, 15.31% in HF ASD group and 42.91% in LF ASD group. To normalize the distributions the RT have been log-transformed, and the means of logRT have been used in the analysis as dependent variable (LogRT). The data distribution has been controlled with Shapiro-Wilk normality test and the homoscedasticity has been assessed with Bartlett's test of homogeneity of variances. Paired t-test was used for post hoc comparison and Bonferroni correction was applied to adjust the significance.

1.4.4.2.1. Within group analysis: as in the analysis of Accuracy, we have firstly explored the effect of Display and Emotion within group. Separately for each group, a 2x3 repeated measures ANOVA has

been computed, with Display and Emotion as within factors. We found that in TD group there was a main effect of Display ($F_{(1,29)}: 4.38, p = .045$) and a main effect of Emotion ($F_{(2,58)}: 3.35, p = .042$), while the interaction was not significant. On the contrary, no significant result was found in both the ASD groups. Results of post hoc comparisons in TD showed that independently of the emotion expressed in the videos, the FLDs were recognized faster than PLDs ($t = -2.784, df = 89, p = .007$). Furthermore, independently of the lighting condition (Display type), fearful stimuli were identified significantly faster than neutral ($p = .012$). In particular, in TD adults the fearful stimuli were recognized more rapidly than Neutral ($p = .012$), but not than happy ($p = .102$). Similarly to the Accuracy data, this results showed that individuals with ASD, irrespective of their IQ level, did not benefit either from the richness of visual features, or from the emotional content conveyed, suggesting that the mechanism coding for BM works differently in this population.

1.4.4.2.2. Between groups analysis: within group analysis has revealed that TD and ASD elaborate the BM differently, but is this elaboration less effective or simply dissimilar? To answer this question we compared the RTs between the three groups. We explored the presence of differences in RTs computing a 3x3x2 repeated measure ANOVA with Functioning as between factor and Display and Emotion as within factors. Results showed significant **main effects of Functioning** ($F_{(2,50)} = 25.48, p < .000$), Display ($F_{(1,50)} = 6.80, p = .012$) and Emotion ($F_{(2,100)} = 4.02, p = .021$), while any of the interaction resulted significant. Overall, **TD adults were faster than both the ASD groups, and HF ASD were more rapid than LF ASD** (all $p < .001$). Moreover, FLDs were identified faster than PLDs ($p = .002$) and fearful expressions were recognized more rapidly than neutral actions ($p < .001$), and marginally than happy ($p = .068$). Permuting post hoc comparisons we found that TD adults were always faster than adults

with LF ASD and HF ASD in identifying all the emotional contents in both the display conditions, but there was no difference between TD and adults with HF ASD in recognizing happy FLDs ($p = .071$).

1.4.4.2.3. Relation between IQ and RTs: Finally, we explored whether the RTs vary according to the IQ level and whether the variation was similar across groups of adult participants. A linear regression model with LogRT as dependent variable and IQ as predictor has been performed separately in each group. We found a significant effect of IQ in predicting the rapidity of responses only in TD group ($F_{(1,28)} = 17.12$, $p = .000$; $R^2 = .38$; adjusted $R^2 = .35$). In either the ASD groups the IQ did not influence the time needed for recognizing the emotional content of BM.

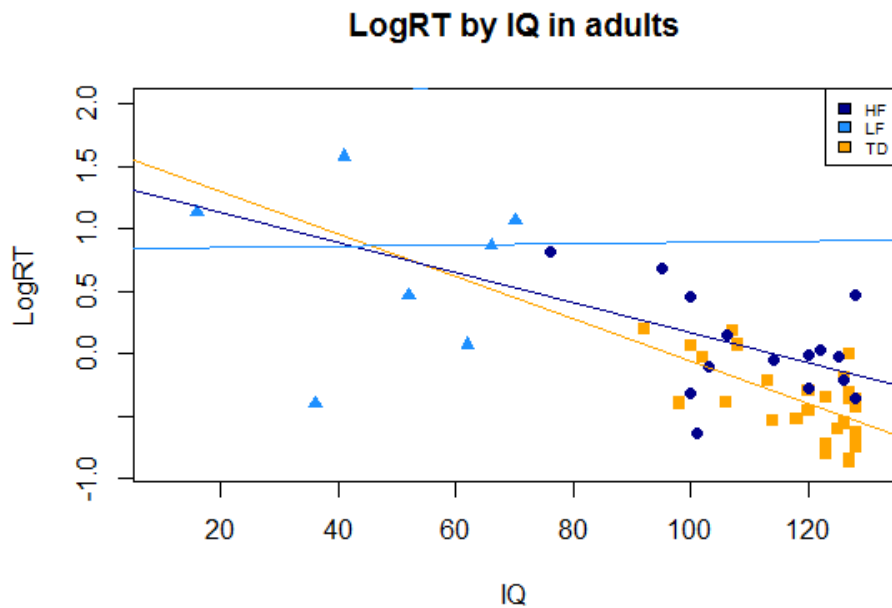


Figure 12. Linear regression between Accuracy and IQ in adults. The dark blue line and circles indicate HF ASD, the light-blue line and triangles indicate LF ASD, the orange line and squares indicate TD.

1.4.5. Discussion

Results of this second experiment are in line with previous researches (Hubert et al., 2007; Nackaerts et al., 2012), and confirm that adults with ASD are impaired in recognizing the emotional meaning of biological motion. Similarly to our results in children, we found that also adults with ASD were less accurate and slower than TD in recognizing the emotional valence of FLDs and PLDs representation of body movements. Results of within analysis confirmed the results of the Experiment 1. We found that in TD adults the identification of expressions of happiness were harder than fearful and neutral movements, and that overall the vision of body form is of help for the comprehension of the emotional valence. On the contrary, in adults with ASD the emotional valence and the richness of visual information did not modulate the Accuracy and the velocity in recognizing the BM stimuli, suggesting that the whole body movements are elaborated differently in ASD than in TD adults.

Comparing the three groups, we found that in adults with ASD the elaboration of BM is not only functionally different, but also less efficient. In fact, the participants with ASD were less accurate and slower than TD adults in recognizing the emotional content of BM. As it was for children, this deficit was present both for emotional and for neutral stimuli, bolstering the idea that the impairment in ASD is more related to the body movement elaboration, rather than being specific for the emotion comprehension.

The majority of the studies exploring the BM perception has used the so called Point-light display as stimuli, a technic that represent the human movement as small lighting dots (Johansson, 1973). This method offers the advantage to isolate the motion information from all the other visual features. To correctly detect this kind of stimuli, a global and integrated perception of all the dots is required. Extensive findings suggest that individual with ASD have difficulties in processing visual information

globally, but they show an advantage in local perception (e.g. Frith & Happé, 1994; Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983, 1993). This particular perceptual style is the core of the Weak Central Coherence theory (WCC) (Frith & Happé, 1994; Happé & Frith, 2006b). The WCC argues that people with autism have an inherent bias towards processing parts of stimuli and an inability to integrate these into a gestalt it has been proposed that deficiencies in BM elaboration in ASD population might be related to a weak central coherence (WCC). In our study we have addressed this hypothesis asking participants to recognize the same exact movement displayed as Point-light or as Full-light video clip and our findings appear partially in contradiction with this theory. If the deficit in BM perception in ASD was related to a weak global perception, we should have found an impairment exclusively in PLDs recognition. In fact, the WCC might explain the impairment showed by children with ASD in processing the PLDs, where the body is represented as few lighting dots. But our participant with ASD showed deficits in understanding also the meaning of FLDs. In FLDs the form of the body is fully visible, there are not elements which necessitate to be holistically integrated. Both in children and adults with ASD, independently from the IQ level, we did not found any difference between PLDs and FLDs either in Accuracy or in RTs. Furthermore, with respect to TD's performance, the ASD impairment was present in either the display condition, suggesting that the WCC may not account for the impairment in BM elaboration – at least not entirely. In our study, we decided to use both FLDs and PLDs because although FLDs are visually more complex than PLDs, they are definitely more realistic. The comparison between the two display conditions enabled us to explore alongside the contribution of a) motion information and b) body form in the comprehension of emotional whole-body movements. In our opinion it is worth noticing that in everyday life we interact with “fully shaped” people, and despite it is indisputable that PLDs stimuli help researchers to study the mechanism for motion elaboration bias-freely, we should

never forget the importance of using realistic stimuli when we want to explain real-life deficiency in clinical population, as it is the impairment in social interaction in ASD.

Another important evidence from our findings regards the use of non-verbal IQ as matching criteria. Non-verbal IQ reflects general cognitive resources that can mediate the acquisition of compensatory mechanisms. Besides, verbal abilities are often lower than non-verbal skills in ASD population, while in healthy population they are commonly balanced. Thus, in our opinion, non-verbal IQ could be a more valid criteria for matching ASD and TD groups - rather than verbal abilities – as it can allow to better detect differences especially between high functioning ASD and TD groups. The direct implication for non-verbal IQ matching is that, to avoid language related bias, the experimental task have to be non-verbal as well. This the reason why in this experiment we asked participants to perform a non-verbal emotional matching task. The problem of using a traditional matching task is that body postures expressing the same emotion are often characterized by similar features and forms. Therefore, a good accuracy in a matching task may not indicate that the emotion has been recognized, but rather participants might have matched stimuli based on visual similarities. As a consequence, studies that did not found difference between ASD and TD using matching task might have not grasped the difficulties of individual with ASD in associating certain nonverbal cues to a specific emotional state. On the contrary, our task required to match the body movements with the respective facial expression, hence there was not the possibility to use visual similarities. To correctly perform the task participants needed to correctly recognise the emotional valence at a more abstract level. Therefore, this body-face matching task allowed us to effectively test the comprehension of the significant conveyed by body movements.

Results of this second experiment showed that a high level of non-verbal IQ predicted the Accuracy in BM recognition in adults with ASD, suggesting that higher cognitive resources are reflected also in highly effective system for BM elaboration. Conversely, RTs are predicted by the non-verbal IQ only in TD adults. Therefore, it seems that high non-verbal abilities might subtend the acquisition of compensatory mechanisms which consent individuals with HF ASD to better comprehend the body language, however this compensation has a cost in terms of time. This suggests that the elaboration of BM information in HF ASD is not immediate and spontaneous as it is in TD, but it is probably mediated by different systems, and it should be computed on purpose by alternative strategies, which take longer to be implemented.

1.5. The development of the ability to recognize the emotional meaning of Biological Motion: a comparison between children and adults in TD population and individuals with high functioning and low functioning Autism Spectrum Disorder.

1.5.1 Introduction

The ability to extract complex information from animate object presented in point light develop very early on (Fox & McDaniel, 1982). 2 days old newborns preferentially orient to biological motion rather than motion of non-biological object (Simion, Regolin, & Bulf, 2008). At 12 months infants are able to extract form from motion information (Fox & McDaniel, 1982) and by five years children perform as well as adults in identifying a body form from moving dots (Pavlova, Krägeloh-Mann, Sokolov, & Birbaumer, 2001). If the BM stimuli are embedded in noise, the adult level is reached a bit later, in adolescence (Annaz et al., 2010; Freire, Lewis, Maurer, & Blake, 2006). In individuals with ASD the ability

to perceive human biological motion seems to be precociously altered. Contrarily to TD controls, children with ASD have been shown not to preferentially attend biological motion either early in development and in young childhood (Annaz et al., 2012). Furthermore, in 8 to 10 years children Blake et al. (Blake et al., 2003) reported that children with ASD were significantly impaired compared to TD children in discriminating PLDs of human walker from scramble dots. Also, the authors found that this difficulty was related to severity of Autism and mental age, while in TD children the chronological age was not correlated with the ability to recognize the biological motion.

All those studies have examined the perceptual abilities in individuals with ASD comparing their performance with control groups matched for age and/or IQ. We did the same in Experiment 1 and 2. This procedure permitted to detect difficulties in ASD population, however it did not provide information on how the ability to recognize the biological motion develops with age. In a recent study, Annaz and colleagues used a cross-sectional design to map developmental trajectories in children with ASD (Annaz et al., 2010). They found a flat developmental trajectory in biological motion processing between the ages of 5 and 12 in children with ASD. Furthermore, by the age of 12 the ASD group was substantially poorer than typical controls at discriminating intact from scrambled Point-Light Displays (PLDs).

Despite copious findings on neutral body movements, very few studies have investigated the developmental changes in the ability of recognizing emotion from the body, both in TD and in ASD population. Studies with typical developing individuals have reported that by 8 years of age children achieved adult performance in recognizing the emotional meaning from dance movements in a matching task (Boone & Cunningham, 1998) and in a forced-choice task (Lagerlöf & Djerf, 2009). When children were asked to freely name the observed emotional body expression the emotion recognition

improved until the beginning of adolescence. For instance, Van Meel and collaborators (van Meel, Verburch, & de Meijer, 1993) investigated the development of recognition of expressive body movement as portrayed by dance (live or videotaped) in children from 5 to 12 years of age. They found that 5 years old children performed worse than other children both in a verbal judgement and in a four forced-choice categorization task of the expressed emotion, suggesting that a child must be at least 8 years old to decode the emotional meaning of an expressive movements. In a force-choice task, Ross and collaborators (Ross et al., 2012) asked to children aged 4 to 17 years and adults to categorize PLDs and FLDs of anger, fearful, sad and happy expressions. They found that children as young as 4 years old performed above chance in decoding affect from body language. Furthermore, they reported a non-continuous development of the ability to identify emotion from body movements. In fact, their data showed that the ability to recognize basic emotion from body movements increased during childhood until 8.5 years and then continued much slower. They also found that adults performed better than children, and in both groups FLDs were recognized better than PLDs. Those results are supported by neuroimaging findings, showing different brain activity in adolescents and adults during the perception of affective stimuli (Peelen, Glaser, Vuilleumier, & Eliez, 2009; Thomas et al., 2001).

With regards to ASD, to our knowledge just one study has investigated the developmental differences in understanding the emotional body language in ASD population. Parron and colleagues (Parron et al., 2008) asked to children and adults with HF ASD and to a group of full-scale IQ matched TD controls to verbally describe PLDs of objects, actions, emotions and subjective states. The authors reported an absence of a developmental trend specifically in emotional processing in autism, while the performance of object, action and subjective state conditions did increase with age.

As I have already pointed out before, deficit in verbal description of body movements in ASD might be due to verbal impairment rather than to deficiencies in visual processing of BM stimuli. Therefore, it could be that individuals with ASD perfectly encode the observed body movement, but they are less skilled than control in using verbal words to describe what they are looking at. The problem with the results in Parron et al. (Parron et al., 2008) is that they might actually reflect this verbal difficulties. The objective of this third study was to overtake this limitation. We explore the ability of recognizing the emotional meaning of human whole-body movements from childhood to adulthood using a non-verbal task. Another criticality in previous studies was the utilisation of point-light representation of biological motion, hence the difficulties emerged so far might reflect WCC perceptual style in ASD rather than deficit in comprehending the meaning of the body movement. To disentangle this issue, in our experiments we also used full-light display, that are more natural stimuli depicting also the body form. Moreover, for the first time we compared developmental changes in individuals with ASD according to different level of functioning. The procedure we have adopted has permitted also participant with LF ASD to perform the task and allowed us to investigate the developmental trajectory in understanding the emotional valence of BM in individual with high and low functioning ASD, compared to changes in TD. To this aim, in this third experiment we compare data collected in Experiment 1 and Experiment 2.

1.5.2 Results

In each group of Functioning we compared the performance between children and adults. A 2x2x3 repeated measures ANOVA with Age as between factor (children vs adults) and Display and Emotion as within factors, was performed in each group of Functioning (TD, HF ASD and LF ASD) both for Accuracy and RTs. Furthermore, we explored the role of IQ and age in modelling the development of BM

recognition in each group. To this aim, we computed regression models with backward stepwise selection, with Accuracy or RTs as dependent variables and IQ and age as regressors. To normalise the data distribution, prior to the analysis the accuracy rate averaged for each participant was arcsine transformed, and the logarithmic transformation was applied over the RTs. Post hoc comparisons were performed with t-test for paired sample and the p-value was adjusted with Bonferroni correction.

1.5.2.1 Comparison between children and adults in TD group:

Analysis of the Accuracy: results showed a main effect of age ($F_{(1,55)} = 14.56$, $p = .001$), a main effect of Display ($F_{(1,55)} = 13.72$, $p = .001$) and a main effect of Emotion ($F_{(1,110)} = 12.45$, $p < .001$). Overall, i) adults were more accurate than children; ii) FLDs were recognized with higher accuracy than PLDs; and iii) fearful and neutral movements were recognized significantly better than happy (both $p < .001$). In particular, post-hoc comparisons showed that adults were always more accurate than children, except in recognizing neutral PLDs where there was not a group difference ($p = .27$). **Analysis of the RTs: results** showed a main effect of age ($F_{(1,55)} = 56.66$, $p < .001$) and a main effect of the Emotion ($F_{(2,110)} = 5.01$, $p = .008$). Post-hoc comparisons revealed that adults were faster than children and that fearful movements were recognized faster than happy ($p = .002$) and neutral ($p = .019$).

Regressions: results of logistic regression in TD group showed a not significant effect of IQ ($p = .847$), the effect of age was marginally significant ($p = .051$) but interaction between IQ and age was significant ($p = .007$). This suggests that in TD group, the IQ itself is not important for the improvement of BM recognition, the age plays a more relevant role (i.e. as they become older, TD people also acquire more expertise and thus identify better the significance of BM), but it is their interaction that defines the development of this ability. The model with IQ and age without interaction is the one that better explained the RTs in TD ($F_{(2,54)} = 37.47$ on 2, $p < .001$; Multiple R^2 : .581, Adjusted R^2 : .565;). This model

showed that both the IQ and the age (both $p < .000$) predicted the rapidity in recognizing the body movements in TD participants.

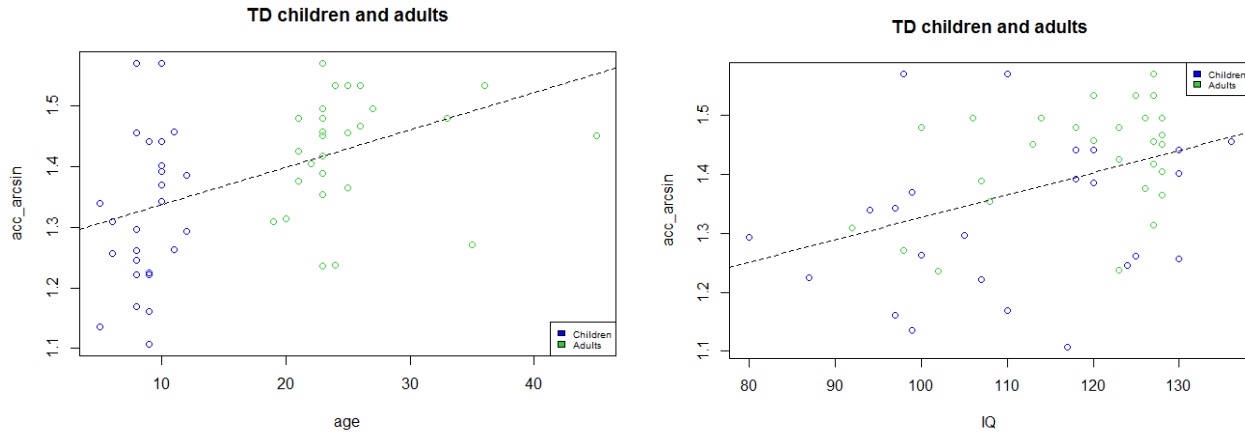


Figure 13. Relation between the accuracy in recognizing the valence of the body movements with age (graph on the left) and with IQ (graph on the right) in TD groups. The blue circles represent the children, the green circles represent the adults.

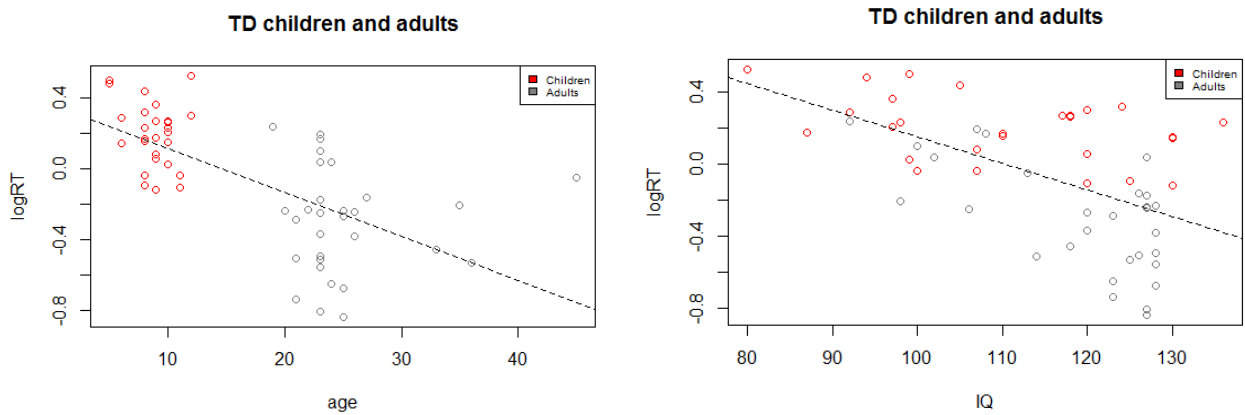


Figure 14. Relation between the rapidity in recognizing the valence of the body movements with age (graph on the left) and with IQ (graph on the right) in TD groups. The red circles represent the children, the grey circles represent the adults.

1.5.2.2. Comparison between children and adults with HF ASD

Analysis of Accuracy: in HF ASD group, results showed a significant effect only for the age ($F_{(1,38)} = 7.26$, $p = .010$), with the adults being more accurate than children. The effect of Display ($F_{(1,38)} = 3.47$, $p = .070$) and the effect of Emotion ($F_{(2,76)} = 2.41$, $p = .096$) were not significant. Despite the effect of Display and Emotion resulted not significant, the p-value was below .01 for both the variables, suggesting a tendency. For this reason, we further investigated this tendency by comparing the levels of the two variables. We found a higher accuracy for FLDs than for PLDs, and Happiness being recognized with less accuracy than Neutral ($p = .028$) and marginally less than Fear ($p = .056$). Post hoc comparisons showed that adults were more accurate than children in recognizing both FLDs and PLDs (both $p < .001$); and emotional (Fear: $p = .006$; Happiness: $p = .001$) but not neutral body movements ($p = .119$). However, when the emotional content was split in the two display conditions, the difference between adults and children remained significant only for happy stimuli (happy FLDs: $p = .029$; happy PLDs: $p = .007$), with adult being more accurate than children.

Analysis of the RTs: in the HF ASD group, results did not show any significant effect.

Regression: the results of logistic regression in HF ASD group showed a significant effect of IQ ($p = .019$), age ($p < .001$) and a significant interaction ($p < .001$), suggesting that not only the experience acquired with age, but also the cognitive level is important in modulating the accuracy in recognizing the emotional valence of BM in HF ASD. The regression with RTs showed that neither the IQ nor the age predicted the rapidity in identifying the emotional valence of BM in HF ASD.

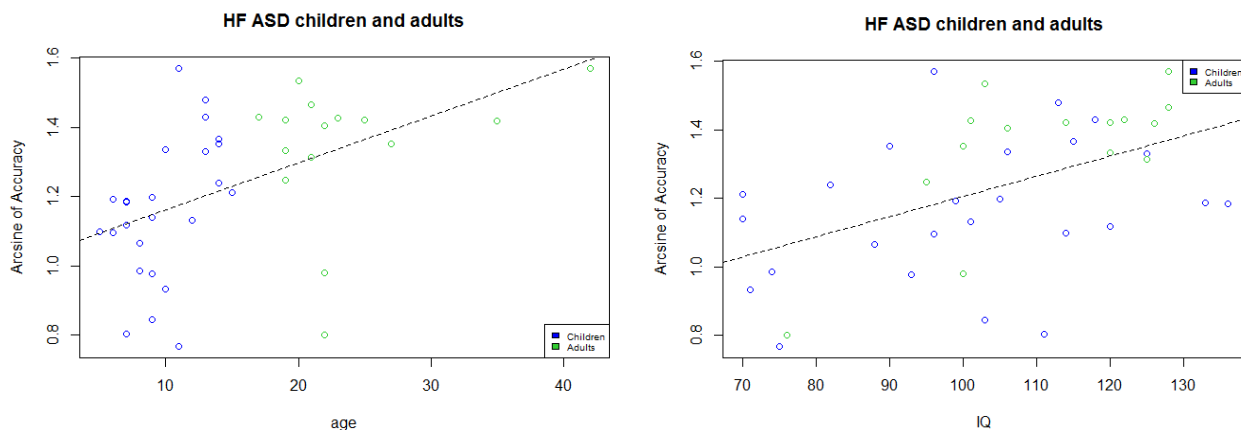


Figure 15. Relation between the accuracy in recognizing the valence of the body movements with age (graph on the left) and with IQ (graph on the right) in individuals with HF ASD. The blue circles represent the children, the green circles represent the adults.

1.5.2.3. Comparison between children and adults with LF ASD: ANOVA in LF ASD group showed a marginally not significant effect of age ($F_{(1,20)} = 3.80, p = .065$) and a marginally not significant effect of Display ($F_{(1,20)} = 3.87, p = .064$). Interesting, the LF ASD children were more accurate than LF ASD adults, suggesting that in LF ASD the ability does not improve with age but, on the contrary, paired-IQ adults seems to have even more difficulties than children in understanding the emotional body language. Similarly to other groups, also in LF ASD the FLDs were recognized better than PLDs.

Analysis of the RTs: results showed a main effect of Display ($F_{(1,21)}: 5.21, p = .033$) and a marginally not significant main effect of Emotion ($F_{(2,42)}: 3.15, p = .053$). Post hoc comparison showed that RT were faster for FLDs than for PLDs, and that Fear was recognized faster than Neutral actions ($p = .004$).

Regression: similarly to HF ASD, also in LF ASD group the logistic regression model showed that either IQ ($p < .001$), age ($p = .01$) and their interaction ($p < .001$) significantly predicted the accuracy. Similarly

to HF ASD, also in LF ASD the regression with RTs revealed that the velocity in recognizing the body movement was not predicted by the IQ or age.

1.5.3. Discussion

To our knowledge, this is the first study comparing the developmental trajectory of the ability to recognize the meaning of biological motion in children and adults with high functioning (HF) and low functioning (LF) ASD and typical controls. Using a forced-choice recognition task, we found a difference in developmental trajectory of the ability to recognize the emotional valence of biological motion stimuli between neurotypical population and individuals with HF ASD and LF ASD. Our results showed that this ability continues to improve with age in TD participants and in participants with HF ASD, while in LF ASD we did not find a significant effect of age. Surprisingly, and oppositely to the other groups, we found that children with LF ASD performed better than low functioning adults.

1.5.3.1 Interpretation of results in TD groups

Our results showed that TD adults are more skilled than TD children in identifying the significance conveyed by body movements. This ability improves and becomes more rapid with age. Furthermore, higher IQ better predicts the performance. Our results in TD participants are in line with previous findings in emotion recognition using FLDs and PLDs body stimuli (Ross et al., 2012). The development of this ability along childhood to adulthood might be linked to a combination of changes in the external social environment and internal developmental changes in the brain structures and the brain activity. During childhood and adolescence, the individual spends a growing amount of time with the group of peers, the occasions for social interaction increase considerably and social exchanges become progressively more complex. Therefore, children learn from experience the importance of non-verbal

communication - such as the body language - and how to interpret social signals conveyed by non-verbal channels. Developmental trajectory of brain structures involved in social and emotion perception seems to be coherent with those changes in external environment. For example, Gogtay et al. (Gogtay et al., 2004) and Guyer et al (Guyer et al., 2008) showed that STS, prefrontal cortex and amygdala undergo developmental changes until late adolescence-early adulthood. The difference between adults and children is also supported by other neuroimaging findings showing different brain activity in adolescents and adults during the perception of affective stimuli (Peelen et al., 2009; Thomas et al., 2001). Moreover, our results corroborate the previous findings that basic emotion are identifiable from body movements, even when form information is eliminated by using PLDS. We found that not only the emotional expression, but also the neutral actions were recognized more accurately when represented as FLDs compared to PLDs, in line with previous researches (Atkinson et al., 2004; Dittrich et al., 1996; Ross et al., 2012). The stimuli we used in our experiments displayed identical body movements, as FLDs and PLDs were created from the same footages. In this way, any possible confound of differences in movement between stimuli condition was eliminated. Among TD participants, both children and adults identified the emotional valence of FLDs more accurately than PLDs, but the vision of body form speeded up the response only in adults. This suggest that in adults there is an over reliance on form information, that might be due to a longer experience in the real world. Instead, in children the neural substrate for coding the signals from the body form is still in developing. It is known that the body form is encoded by two areas: the Fusiform Body Area (FBA) in the Fusiform gyrus (Peelen & Downing, 2005), and the Extrastriated Body Area (EBA) in the occipital-temporal cortex (Downing, Peelen, Wiggett, & Tew, 2006). Those areas partially overlap with the brain regions coding for the face stimuli (fusiform face area-FBA and occipital face area-OFA). Recent developmental fMRI studies have provided evidence

for developmental changes in late childhood (Aylward et al., 2005; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Golarai et al., 2007; Passarotti et al., 2003; Scherf, Behrmann, Humphreys, & Luna, 2007). Also, those studies reported that FFA was larger and more face-selective in adults than children. Since body and face areas occupy nearly identical cortical site in human brain, it is plausible that also body selective area follow the same developmental trajectory. On the contrary, the region coding for the biological motion are reported to be immediately tuned after birth and to mature early in childhood (e.g. Pavlova et al., 2001). Those previous findings suggest that in TD children the human motion information is encoded easily, while the neural structures processing the form of the body are still not completely specialized. This might explain why we did not found differences in RTs between FLDs and PLDs in TD children, but faster recognition of FLDs in adults.

1.5.3.2. Interpretation of results in ASD groups

The development along childhood to adulthood might be linked to a combination of changing in the external social environment and developmental changes of brain structure and brain activity. However, individuals with ASD have less occasion to train this ability on the ground as they tend to avoid social situations, or to make experience of distorted and often unsuccessful interactions. This atypical estrangements from social cues start early in life: children as young as 15 and 24 months do not preferentially attend to human movements (Klin et al., 2009; Klin & Volkmar, 2003). Furthermore, the adolescence is the period during which social interactions become more significant and frequent, but adolescent with ASD do not preferentially attend to social visual cues (Klin, Jones, Schultz, Volkmar, & Cohen, 2002). This lack of experience is also reflected at the neural level. Indeed, neuroimaging findings have reported abnormal activity of brain regions deputed to BM perception in children and adults with ASD (Freitag et al., 2008; Herrington et al., 2007; Kaiser et al., 2010; McKay et al., 2012; Nackaerts et

al., 2012; Weisberg et al., 2014). These researches suggest that there may be a dysfunction in biological motion processing amongst people with ASD, that is still clearly evident at a young age, but that may be hidden by compensatory mechanisms later in life. These mechanisms may be due to adults with ASD accomplishing the same tasks using different brain regions and pathways, which have adapted to compensate these functions. Coherently with those hypothesis, we found an improvement in comprehending body movements in HF ASD which was associated with age and non-verbal resources suggesting that people with ASD used alternative strategies for inferring social signals to body movements. On the contrary, the rapidity was not predicted by age and marginally not by IQ, suggesting that although the compensatory strategies become more efficient with age, they continue to have a cost in terms of time. Evidence from neuroimaging studies seems to corroborate this hypothesis. For example, McKay and collaborators (McKay et al., 2012) reported different connectivity between areas coding for the biological motion. They found that TD used a unitary network, where the motion information is transmitted from temporal to parietal region. On the contrary, individuals with ASD used two different network, respectively including motor and form selective areas. Moreover, they showed that the connection between temporal and parietal areas is missing in ASD. The authors suggested that this might be due to white matter abnormalities in early childhood, hence to achieve TD-comparable levels of BM processing, individuals with ASD recruit independent cortical network. Those findings might also explain why we did not find differences in accuracy and RTs between display conditions in LF ASD. In fact, PLDs and FLDs require the elaboration of motion and motion+form information (Giese & Poggio, 2003). In TD individuals, these information are integrated in an interconnected neural network. When PLDs are perceived, the form from motion has to be extracted, while in FLDs the form is already visible, thus no further cognitive abstraction is needed. For this reason, in TD the process of

FLDs is more accurate and faster. On the contrary, in people with HF ASD form and motion cues remain isolated and are processed in distinct brain region. There is not advantaged from integration because of the lack of connectivity between area for motion and form perception, therefore the accuracy and velocity do not differ between different display conditions.

Furthermore, in individuals with LF ASD we did not observed any developmental improvement, on the contrary adults with LF ASD performed even worse than children with LF ASD. This different developmental changes between HF and LF ASD suggest that the ability to compensate deficit in body movement understanding is mediated by non-verbal cognitive resources. Neuroimaging findings showed that in TD individuals the maturation of widely distributed brain function might underlie cognitive development (Luna et al., 2001). This could be true also for people with ASD. Future investigation are needed to explore the relation between the executive functions and ability to identify the meaning of human movements in individuals with ASD. The findings of a correlation with neuropsychological profiles characterized by high executive functions and activities in frontal lobe would be in favour of our hypothesis.

Chapter 2

DEFICIT IN EMOTION RECOGNITION IN HIGH FUNCTIONING AUTISM SPECTRUM DISORDER: A COMPARISON BETWEEN FACIAL AND BODILY EXPRESSIONS

2.1. Introduction:

The emotional expressions convey attitudes, feeling, and intention of people around us. Hence their comprehension is crucial for successful social interactions. The other way around is also true, the experience with social environment foster the development of the ability to interpret the emotional signals (Leppänen & Nelson, 2006). In a virtuous circle, being in contact with people improves the ability to comprehend them and, in turn, a better comprehension of others increases the number of successful and rewarding social exchanges, promoting new interaction seeking. The Autism Spectrum Disorder (ASD) is a neurodevelopmental disorder characterized by deficits in social-emotional reciprocity; deficits in nonverbal communicative behaviours used for social interaction; and deficits in developing, maintaining, and understanding relationships (DSM 5, APA 2013). Not surprisingly the ability to recognize the emotions is a core deficit of this syndrome and it has been described as distinctive since its original treatise (Kanner 1943). However, the exact nature of the emotional deficits in ASD remains unclear. For decades, researchers have investigated the perception of emotional expressions in ASD, yet no consensus has emerged and the overall evidence remains mixed. Difficulties in recognizing emotional facial expression in children with ASD were often reported in studies matching controls and ASD groups for nonverbal skills (Bormann-Kischkel, Vilsmeier, & Baude, 1995; Macdonald et al., 1989a; Tantam, Monaghan, Nicholson, & Stirling, 1989). However, no differences in facial emotion recognition between ASD and TD groups clearly emerged when verbal IQ was used as matching criteria (Castelli

2005; Davies et al. 1994; Loveland et al. 1997). A reduced accuracy in recognizing emotional facial expression has been reported also in adults with ASD, especially for negative emotions (Ashwin, Chapman, Colle, & Baron-Cohen, 2006a; Bal et al., 2010; Howard et al., 2000; Wallace, Coleman, & Bailey, 2008). In particular, individuals with ASD performed significantly worse than controls at verbally identifying fear. Furthermore, Ashwin and collaborators (Ashwin, Wheelwright, & Baron-Cohen, 2006) found that the individuals with Asperger's Syndrome responded slower to faces than to non-social stimuli (such as objects), regardless of the emotional expression or the sex of the actor. Such difference was not found in the control group, suggesting a specific impairment in faces processing in ASD. Researches on emotion recognition in ASD has traditionally been focused on facial expression, however faces are not the only channel to communicate emotional or social relevant information. Probably, the interest for faces is related to their primary role in conveying social signal when the interlocutors are close, but it has been demonstrated that bodies are as important as face (de Gelder et al., 2010; de Gelder, 2006) – or even more (Aviezer & Todorov, 2015; Van den Stock et al., 2007) - in conveying emotional cues. Of late, it has been growing interest in exploring the perception of body movement in people with ASD. The majority of the studies have investigate the encoding of body movement using the so called point-light display (PLDs), consisting in few illuminated dots placed over the major joints of a moving person who is video recorded in a dark set (Johansson, 1973). When neutral stimuli are presented, conflicting results have been reported: some studies have found impairment associated with ASD (Annaz et al., 2010; Blake et al., 2003; Kaiser & Pelphrey, 2012), while others have not (Freitag et al., 2008; Herrington et al., 2007). However, deficits in emotion recognition are consistent and systematically reported in young children (Moore et al., 1997), adolescents (Hubert et al., 2007; Parron et al., 2008) and adults (Atkinson, 2009; Nackaerts et al., 2012) with ASD. Yet it is not clear if the

difficulties in social interaction in individual with ASD are related to a general impairment in the processing of biological motion, to a selective deficit in emotion recognition, or both. Furthermore, although PLD stimuli offer the advantage to isolate motion information from all the other visual cues - hence a unique opportunity to study the role of movement in conveying social meaningful cues - it is undeniable that they are not properly ecologically valid. To overtake this issue, Atkinson and collaborators (Atkinson, 2009) compared the recognition of emotions between traditional PLDs and more ecological full-display of the same movements (FLDs). They found that ASD were less accurate than controls in identifying happiness, anger and disgust, and marginally less accurate for fear and sadness in both FLDs and PLDs. Since the two classes of stimuli depicted exactly the same actions, this result suggests that deficit in emotion recognition might be related to abnormalities in motion processing, irrespective of visual body form information. In line with this finding, it has been proposed that poor motion perception may interfere with emotion recognition in whole moving bodies (Dakin & Frith, 2005). To reduce the impact of motion perception, recent studies have explored the encoding of emotional body movements using static stimuli. Again, evidences are discordant. Peterson and collaborators (Peterson, Slaughter, Brownell, & Peterson, 2015) found that the ability to recognize emotions from body postures did not differs between children with ASD and TD controls, while ASD performed significantly worse than TD when they were asked to recognize the emotion from eyes and in a Theory of Mind task (the authors utilized the false belief tests (Baron-Cohen et al. 1985) and the Theory of Mind Scale (ToM Scale) by Wellman & Liu, 2004). The authors also found that age, but not verbal IQ, correlate with recognition of bodily expressions in both groups. In a fMRI study (Libero, Stevens, & Kana, 2014), a group of adolescents and young adults with high-functioning autism (HF ASD) were asked to recognize emotional and neutral body postures depicted as stick figures characters.

Despite a different pattern of neural connectivity between ASD and controls, results showed no differences in brain activation and in the behavioural task (nor in accuracy nor in response times) between groups. Also, in this experiment both groups recognized the emotional body postures worse and slower than the neutral. Opposite results come from studies in adults with ASD, where differences between ASD and TD in recognizing emotional body language clearly emerged. For example, comparing static images of neutral and fearful actions, Hadjikhani and collaborators (2009) found that ASD group recognized neutral action better than TD, but they scored lower in the emotion condition (fear). A different study (Doody & Bull, 2011) has tried to move beyond the deciphering of basic emotion, investigating the decoding of more subtle mental states from body postures - such as boredom, interest and disagreement - in adults with ASD. The authors found a deficiency in verbal labelling of boring posture in ASD, while in a matching test no differences between groups emerged. Individuals with ASD tend to have obsessive interests and to ramble on others without realizing that they are tedious, and the authors suggested that this lack of awareness could be linked to a deficit in interpreting body postures.

As I have already pointed out, emotional and social meanings are transmitted through several nonverbal channels. If it is true that people with ASD have difficulties in understanding emotional signals, is this impairment extended to all those mediums or is it restricted to some of them? Also, is the difficulty broadened across different domains or is it more severe for specific type of stimuli? To date, the deficit in recognition of emotions across stimulus categories is mostly unexplored. Few studies have directly compared the recognition of facial and bodily expressions (Doody & Bull, 2013; Philip et al., 2010; Weisberg et al., 2014), showing a deficit in emotion labelling in people with ASD both for faces and body movements (but see also Actis-Grosso, Bossi & Ricciardelli, 2015). Using images of facial

expressions and bodily emotions performed by avatars, Doody and Bull (2013) found that adolescents with Asperger's Syndrome (AS) were as accurate as controls in a matching task both with face and body expressions, but they showed difficulties in choosing a verbal label for the same stimuli. Especially, participants with ASD were significantly poorer in identifying bodily emotion of fear. Interestingly, the fear-related difficulties were specific for body postures, as the two groups did not differ in matching or verbally label fearful faces. Also, ASD group did not differ from controls on overall time taken to respond in verbal labelling task, but they took longer in matching body posture of anger. Altogether, this results suggest a difficulty in ASD group related to negative stimuli. In line with that, Philips and collaborators (Philip et al., 2010) found deficit in identifying fearful body movements. The authors use the Wechsler Abbreviate Scale of Intelligence as matching criteria and compared the recognition of emotional images of faces, videos of bodies, and voices. They found that ASD were less accurate than TD in recognizing the emotions in all the stimulus domains, either visual or auditory, static or dynamic. In particular, ASD recognized worse facial expression of anger, and bodily postures of fear and happiness. However, using the same matching criteria (WASI), Libero and colleagues (Libero et al., 2014) reported no group difference in emotional body recognition. Another study compared the recognition of emotional images of faces and dynamic PLD in people with high (HAT) and low level of autistic traits (LAT) (Actis-Grosso et al., 2015). The authors found no difference between the two groups in recognizing PLDs representing non-emotional actions, suggesting that the ability to integrate the moving lighting dots into a holistic configuration is integer in individuals with HAT. Moreover, the authors found faster RTs for happy faces (compared to other facial expressions) in both LAT and HAF group, while the same advantage for happy stimuli was present only in LAF group in emotional PLDs recognition. Finally, their results showed that LAT recognize fear with higher accuracy when conveyed by PLDs, while sadness

were recognized more accurately when conveyed by facial stimuli. On the contrary, in HAF group fear was recognized better from faces than from PLDs. According to the authors, these results suggest that HAT might rely on different cues from those used by LAT in emotion recognition, they seem to rely more on static face details than on bodily kinematic cues.

Another critical issue to disentangle the nature of social deficits in individuals with ASD is related to the function and dysfunction of motion processing in relation to emotion comprehension. How demanding is the elaboration of motion information for individuals with ASD? And how does it influence the recognition of emotional bodily expressions? To answer this questions, one study has investigate the difference in perceiving static or dynamic stimuli in ASD (Weisberg et al., 2014). Results revealed no group difference between ASD and controls in response to either static or dynamic faces, bodies or objects at a behavioural level. Though, the stimuli used in this study were emotionally neutral. Furthermore, the only group difference in brain activation across stimuli was related to the right fusiform gyrus (FG), suggesting a deficit of connectivity in ASD brain between social related areas and FG.

Contradictory results in participants with ASD may be due to several factors, such as IQ matching criteria, age, task demands and stimulus type (e.g. static or dynamic). With regards to IQ, the ASD includes a broad clinical phenotype and encompasses a wide degree of intellectual deficit. People who match criteria for the autism spectrum but do not show intellectual impairment (i.e. intelligent quotient (IQ) above 70) are commonly referred as high-functioning ASD (HF). Especially in this individuals with high cognitive resources, deficits in social communication and difficulty in understanding other people in everyday interaction are the most debilitating issues. Those clinical and personal reports are partially

confirmed by scientific findings. Some studies showed deficits in children and adults with ASD in recognizing facial expressions, however results remains mixed (Harms, Martin, & Wallace, 2010). One explanation for this contrasting findings sees individual with HF ASD compensating emotion recognition deficits with other higher cognitive processes (Belmonte and Yurgelun-Todd, 2003). They might adopt different compensatory mechanisms depending on the task or the stimulus type. Therefore, even when the identification of emotional expressions is similar between controls and HF ASD groups, it is not possible to rule out the possibility that the encoding of this stimuli is altered.

Another factor that could explain discrepancies in previous studies is the criteria adopted for matching intellectual ability between participants with ASD and controls (Burack, Iarocci, Flanagan, & Bowler, 2004). In the majority of studies groups were matched according to verbal skills, but the cognitive profile of people with ASD is commonly uneven, with verbal abilities lower than nonverbal. Therefore, it is likely that individual with ASD have higher nonverbal abilities than control participants with the same verbal IQ.

Taken together the listed studies reported conflicting results, varying significantly according to matching criteria, stimuli, and tasks. In particular, deficit in emotion recognition in individuals with ASD emerges when the nonverbal IQ is used as matching criteria. Critically, the majority of studies have investigated the comprehension of emotions using a single class of social stimuli, such as faces or bodies solely. Thus, the existence of an impairment across stimulus domains is mostly underexplored in individuals with ASD. Finally, it is not clear whether the impairment in social interaction is related to motion or emotion processing. In the present study we tried to fill those gaps, investigating the ability to understand emotions across a range of different social signals – such as facial and bodily expression - in the same group of subjects with HF ASD. We firstly compared the recognition of facial and bodily

expressions using static pictures. Then we used dynamic (video clips) and static (images) stimuli to explore the role of motion perception in emotional body movement comprehension. Finally we investigate the importance of perceiving the body form comparing dynamic body expression represented as FLDs and PLDs. Importantly, participants in ASD and control groups were matched for nonverbal IQ.

2.2. Methods

2.2.1. Participants: 20 subjects with HF ASD (all males, age M = 19.85; age SD = 7.07; IQ M = 116.85; IQ SD = 10.03) and 20 controls matched for non-verbal IQ, age and gender (2 females and 18 males, age M = 20.44; age SD = 5.27; IQ M = 123.45; IQ SD = 8.68) took part in this experiment. All participants have normal, or correct-to-normal vision. All participants with ASD met the established criteria specified in DSM-IV (American Psychiatric Association 2006) or DSM-5 (American Psychiatric Association 2013). The diagnosis was confirmed using the Autism Diagnostic Observation Schedule (Lord et al. 2000) and/or ADI (Lord, Rutter, & Le Couteur, 1994). Non-verbal IQ scores were measured with the Raven's progressive matrices (Raven 1936). Before the experiment, participants received an exhaustive explanation of the experimental procedure and were asked to read an informative form. Informed written consent was obtained from each participant or their parents prior to the experiment, according to the Declaration of Helsinki. The study was approved by the ethical committee of the University of Milano-Bicocca. Participants with ASD were recruited from the Observation, Diagnosis and Education Laboratory at the University of Trento.

Group	Age		IQ	
	M	SD	M	SD
ASD	19.85	7.77	116.85	10.03
TD	20.44	5.27	123.45	8.68

Table 4. Descriptive statistic of participants in the main experiment

2.2.2. Stimuli: in the present experiment we use pictures of facial and whole-body depicting neutral and emotional expressions, and video clips of point-light (PLDs) and full-light display (FLDs) of neutral and emotional body movements.

2.2.2.1. Images of Body movements: a set of novel pictures depicting emotional and non-emotional body movement has been created by our group. The initial dataset included bodily expressions of fear, happiness, anger, sadness and neutral actions but to the purpose of the present experiment we selected only happy, fearful and neutral movements. We asked to a total of 8 nonprofessional actor (4 Italian Caucasian males and 4 Italian Caucasian females) to express the aforesaid emotions moving their whole body, or to perform emotionally neutral instrumental actions (kick, run, pick up, push, wear a socks). For the emotional expressions, the actors received examples of potential scenarios, such as joyful (e.g. your team has just scored and won the final match) or threatening (e.g. a giant spider is falling down over you) situations. To reduce any possible clothes-related bias, all the actor wore blue jeans, a white t-shirt with long sleeves and light tennis shoes. Every picture showed one single actor, presented over a black background. To focus exclusively on information conveyed by the body, the faces were blurred in all pictures.

2.2.2.1.1. Pilot study: Prior to the main experiment, we run a pilot study to assess the effective recognizability of 48 emotional bodily expressions (12 for each emotion) and 60 neutral movements (12 for each type of action). We asked to 20 typical developed (TD) adults (4 females and 16 males, age $M = 24.65$, age $SD = 1.66$) to recognise the emotional content of every pictures in a multiple forced choice task, and subsequently to rate the intensity of the emotion expressed in a 5 point scale. Emotional and neutral movements were presented in two separated blocks, the order of presentation was counterbalanced between participants, and within each block the images were presented randomly. Responses were given by keyboard and participants were asked to use their right hand to answer. Every trials started with one-second fixation cross, then the image appeared and lasted for maximum 3 seconds. The image was always presented in the centre of the screen; the task question appeared above the image; the response options were presented below the image. In the block “emotions”, the question presented on the top of the screen was “Which emotion?” and participants could choose between 5 response option options (Fear, Happiness, Anger, Sadness, plus the option Other) corresponding to the keys “F, G, H, J, K”. A sticky label with the initial of every response option identified the response keys. The correspondence between keys and response option were randomized across participants. When participants responded, a second slides with the question “How intense was the expressed emotion?” was presented together with the rating scale, where 1 corresponded to “not at all” and 7 to “extremely”. To rate the images, participants were asked to use the key number from 1 to 7 on the of the keyboard. The procedure in the “neutral” block was the same. Above the images was presented the question “Which actions?” and on the bottom part of the screen the 6 options (the five abovementioned actions, plus the option “Other”). Since the images were emotionally neutral actions, participants did not rate the emotional intensity but we simply asked them to judge whether the

performed action was an emotion or not. They could answer “yes” or “no” using the keys “B” or “N”. Participants of the pilot study were students at the University of Milano-Bicocca in Milan or friends of them. All participants volunteered and signed an informed consent before starting the experiment, according to the Declaration of Helsinki. All participants were tested individually in a quiet room. They seated in front of an Acer notebook, with display dimension 34x19x40, located approximately at 60 centimetres from the observer. All the stimuli were presented at the centre of the screen. The experimental procedure (stimuli presentation and responses registration) was implemented with the software E-Prime 2.0®.

This dataset of pictures was created to explore the recognition of bodily expressions in people with ASD, who notably have difficulties in recognizing emotions. For this reason we needed a set of images sufficiently recognizable also for participants with ASD, but not obvious to try to avoid the ceiling effect in neurotypical subjects. We select stimuli whose accordance about the expressed emotion ranged between 80 and 100%. For the emotional expressions, we choose fearful and happy stimuli whose intensity was rated above 4.7; for the neutral actions, we selected stimuli that was never confounded as an emotion.

2.2.2.2. Images of Facial expressions: face stimuli were selected from the Radboud Faces Database (Langner et al., 2010). This dataset includes images of Caucasian Dutch actors rated on a scale from 1 to 5 for the actor’s attractiveness; the percentage of agreement on emotion categorization; intensity and genuineness of the facial expression; and valence. We selected images of neutral, happy and fearful expressions. Each emotional category included pictures of 4 adult females and 4 adult males with frontal gaze direction and frontal head orientation. Facial stimuli were selected according the

following criteria: index of clarity above 3.5/5; agreement above 80/100; finally the stimuli were matched for attractiveness of the actor and emotional intensity across all the emotional categories.

2.2.2.3. Videos of point-light (PLDs) and full-light (FLDs) display: the same stimuli used in previous experiment (Experiment 1, 2, and 3 in Chapter 1) were presented also in the present Experiment. They consist in short video clips depicting emotional and neutral whole-body moments as FLDs and PLDs and they were realized by Atkinson and collaborators (Atkinson et al., 2004, 2012). Please see Chapter 1 for stimuli description and rating procedure.

2.2.2.4. Final set of stimuli: the goal of the present study was to explore the difference between people with HF ASD and TD in recognizing the emotional content conveyed by various classes of social stimuli (static facial and bodily expression and static and dynamic emotional body movements). For this reason, we needed that the stimuli in the different classes were equally recognizable. The correct identification of the stimuli should be related to the effective recognizability of a class of stimuli rather than a different level of emotional intensity across classes. To this aim, we matched the stimuli according to their emotional intensity, across all the classes in every emotional category. The four classes of stimuli were rated using different scales (5 point scale for facial expressions; 7 point scale for bodily expressions; 9 point scales for PLDs and FLDs). Therefore, to match the emotional intensity across the different classes of stimuli we used a proportion to transform the rated intensity of faces and bodies images in a 9 point scale. The final set of stimuli was formed by 24 items for each class (8 neutral, 8 fearful and 8 happy), for a total of 48 static (24 faces and 24 body movements) and 48 dynamic stimuli (24 FLDs and 24 PLDs).

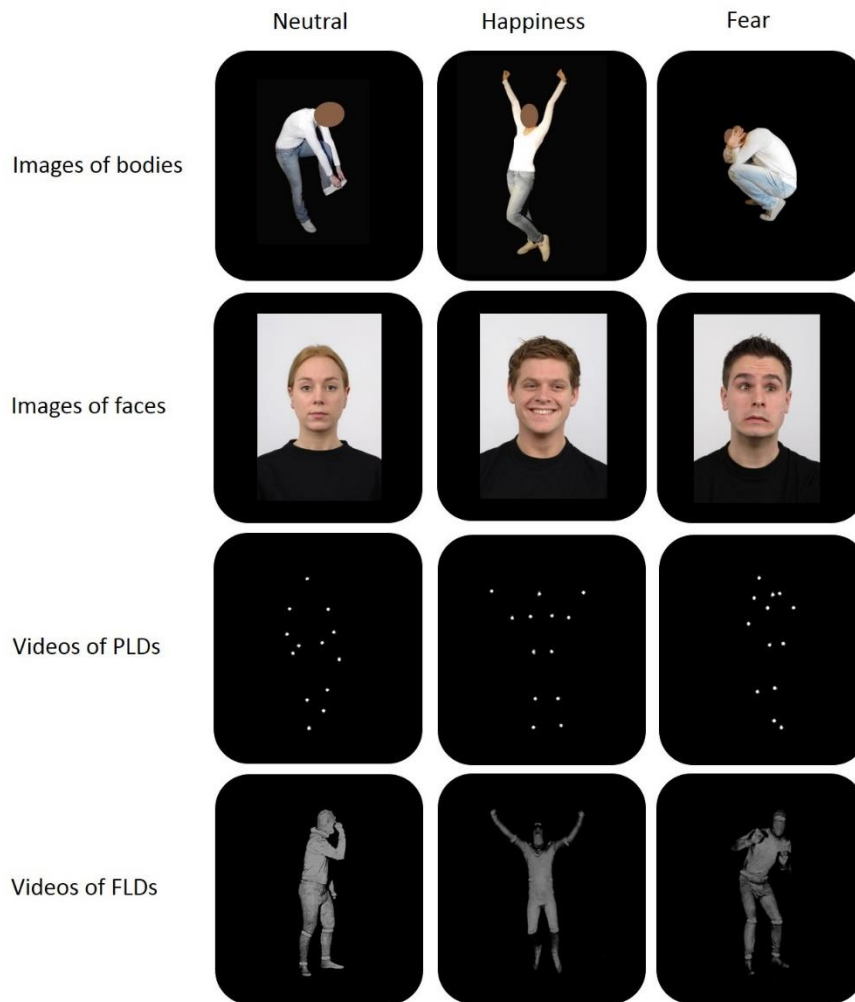


Figure 16. Example of the stimuli

2.2.3. Procedure: all participants were asked to categorize four classes of stimuli: images of faces, images of whole body, and video clips of full-light (FLDs) and point-light display (PLDs) of whole body movements. The stimuli could depict emotion of fear, happiness or neutral expression. Every stimulus category has been presented in a separated block, for a total of 4 blocks administered to each participant. Each block lasted around eight minutes, and the order of block presentation was counterbalanced between participants. In total, each participant saw 30 PLDs (10 fearful, 10 happy and 10 neutral movements); 30 FLDs (10 videos for each emotional category as the PLDs); 24 images of facial expressions and 24 images of whole body expressions (8 trials per emotional category, both for

facial and for body expressions). As explained above, the facial expressions were selected from the Radboud Faces Database (Langner et al., 2010); the videos were realized by Atkinson and collaborator (Atkinson et al., 2004); the images of whole body expressions were realized by us. The duration of the stimuli was 2 seconds for the PLDs and 3 seconds for the FLDs. To maintain coherence across stimulus conditions, the images were presented for 3 seconds as well. Every block started with few practice trials, to allow participants to familiarize with the stimuli and with the task. Every trial started with a one-second fixation cross, then the stimulus was presented for 3 seconds. The question “Which emotion?” was printed on the top part of the screen and the response options on the bottom; both lasted until participants responded. Responses were collected by keyboard, and the order of key-emotion correspondence was randomized across participants. Accuracy and response times (RT) were recorded. The experimental procedure (stimuli presentation and responses collection) was implemented with the software E-Prime 2.1. At the end of the experiment, participants were administered the Matrix of Raven test to assess the IQ level.

2.3. Results

Accuracy rate (Accuracy) and response times (RTs) were considered in the analysis. As index of Accuracy, the percentage of the correct responses over the total of stimuli presented was calculated for every emotional condition, of every display, in all participants.

2.3.1. Analysis of Accuracy

Between group comparisons: We firstly explored differences between participants with ASD and TD controls. Overall, a Pearson's Chi-squared test with Yates' continuity correction showed no differences between individuals with HF ASD and TD in recognizing the emotional content of social-relevant stimuli

($\chi^2 = 1.09$, $df = 1$, $p = .296$). ASD did not show an impairment in understanding the meaning of facial expressions ($p = .577$), FLDs ($p = .223$), PLDs ($p = .498$) or static body images ($p = .743$). Also, we did not find any group difference in recognizing fearful ($p = .329$), happy ($p = .179$) or neutral stimuli ($p = .465$).

	ASD				TD			
	FLDs	PLDs	Body images	Face images	FLDs	PLDs	Body images	Face images
Fear	97.25	93.25	98.44	96.56	94.75	94.10	96.250	97.19
Happiness	92.00	92.00	94.69	98.12	92.25	87.50	94.375	97.81
Neutral	97.50	95.25	93.75	96.25	96.25	96.67	95.00	97.50

Table 5. Percentage of Accuracy, subdivided by groups, class of stimuli (columns), and emotional category (rows).

Within group comparisons: Subsequently, within group logistic regressions were performed to compare the level of accuracy between stimulus type and emotional category separately in each group.

First, we explored if there was a class of stimuli which better conveyed a specific emotion (i.e. happiness better recognize from facial expression or fear more accurately identified from bodies).

Comparing the accuracy across **fearful stimuli**, we found that ASD participants have difficulties in recognizing the PLDs: fearful PLDs' accuracy was significant lower than fearful FLDs ($p = .010$), fearful body ($p = .002$), and marginally than fearful face ($p = .052$). This suggests that ASD have difficulties in recognizing the significance of body movement when it is dynamic and the body form is not visible. No other difference was found in fearful stimuli between faces, bodies and FLDs.

In TD group the only difference - although marginal - was between fearful faces and fearful PLDs ($p = .0538$), with this latter recognized with lower accuracy, suggesting that in TD participants the accuracy in recognizing body movement was similar, either dynamic or static, with visible or not visible body form.

When the emotion expressed was **happiness**, in participants with ASD the images of happy faces were recognized better than all the other happy stimuli: accuracy was significantly higher either than happy body image ($p = .025$), or than the happy dynamic stimuli ($p = .001$ both for FLDs and PLDs). There was not any difference in accuracy between happy body images, PLDs, and FLDs, suggesting that the stimuli depicting happy body expressions are encoded similarly.

Also in TD group, happiness was recognized better when conveyed by faces and worse when conveyed by PLDs. Indeed, accuracy for happy facial expressions was higher than happy body images ($p = .030$), happy FLDs ($p = .002$) and happy PLDs ($p < .000$). Besides, accuracy of happy PLDs was significantly lower than happy FLDs ($p = .027$), happy body images ($p = .002$), and happy faces ($p < .000$). Accuracy between happy FLDs and happy body images did not differ.

Finally, when the stimuli portrayed **neutral** actions, individuals with ASD identified FLDs significantly better than neutral body images ($p = .006$), marginally better than neutral PLDs ($p = .084$) and not differently from neutral faces. In TD group we didn't find any difference in the accuracy between the different classes of neutral stimuli.

Comparing the accuracy relative to each stimulus category across the different emotional contents, we found that:

- In ASD, the images of fearful **body** were recognized significantly better than images of happy ($p = .014$) and neutral body ($p = .005$), while we did not find any difference between images of happy and neutral body movements. Additionally, fearful and neutral **FLDs** were recognized with higher accuracy than happy FLDs ($p = .001$ and $p = .009$ respectively), but they did not differ between each other. Similarly, in **PLDs** the Happy stimuli were recognized worse than neutral ($p = .022$). However, no differences between fearful and happy PLDs, or fearful and neutral PLDs emerged. Finally, no difference was found between emotional valences in facial expressions recognition.
- In TD, happy PLD were recognized significantly worse than fearful ($p = .002$) and neutral PLDs ($p < .000$). Similarly, happy FLDs were recognized with less accuracy than neutral FLDs ($p = .017$). Finally, we did not find any difference across emotional contents for face nor for body accuracy.

2.3.2. Analysis of Response Times (RTs)

In the analysis of the Response Time (RTs) only the correct responses were considered. The percentage of excluded item corresponded to 3.69% of the images and 5.46% of the videos in the ASD group; 3.66% of images and 6.42% of video in TD group. To normalize the distribution, the RTs were log transformed before the analysis. Repeated measures ANOVAs were performed to compare RTs across conditions, within and between groups. Emotion (fear, happiness and neutral) and display (face, body, FLDs and PLDs) were always considered as within variables, and group (ASD and TD) as between variable. Post

hoc comparisons were permuted using pairwise t-test for paired sample and p-values were adjusted with Bonferroni's correction.

2.3.2.1. The first research question we aimed to answer was whether there exist a difference in recognizing the emotions expressed by face or by body.

Within group comparison: We initially explored the existence of differences in identifying the emotional content from facial or bodily expressions. To compare the RTs relative to images recognition, a 2x3 repeated measures ANOVA with class of stimuli (face and body) and emotions as within variables was performed separately in TD and ASD group.

TD: In TD group we did not find any significant difference between images of bodies and faces. Results showed no significant effects nor for display ($F_{(1,19)} = 1.209$, $p = .285$), emotions ($F_{(2,38)} = 1.709$, $p = .196$), or interaction ($F_{(2, 38)} = .427$, $p = .655$), suggesting that the time needed to infer the emotional significance is similar for facial and body expressions.

ASD: in ASD group we found a main effect of display type ($F_{(1,19)} = 16.18$, $p > .000$), with faces recognized faster than bodies, and a significant interaction ($F_{(2,38)} = 4.14$, $p = .024$). Post hoc comparison showed that fearful faces were recognized significantly faster than fearful bodies ($p = .003$) and neutral faces faster than neutral bodies ($p = .001$). No differences in RTs were found between body and face when the expressed emotion was happiness. The effect of the emotion ($F_{(2,38)} = 2.40$, $p = .104$) was not significant. In fact, post hoc comparison did not show any significant difference between the emotional content of faces and bodies (all comparisons $p > .06$).

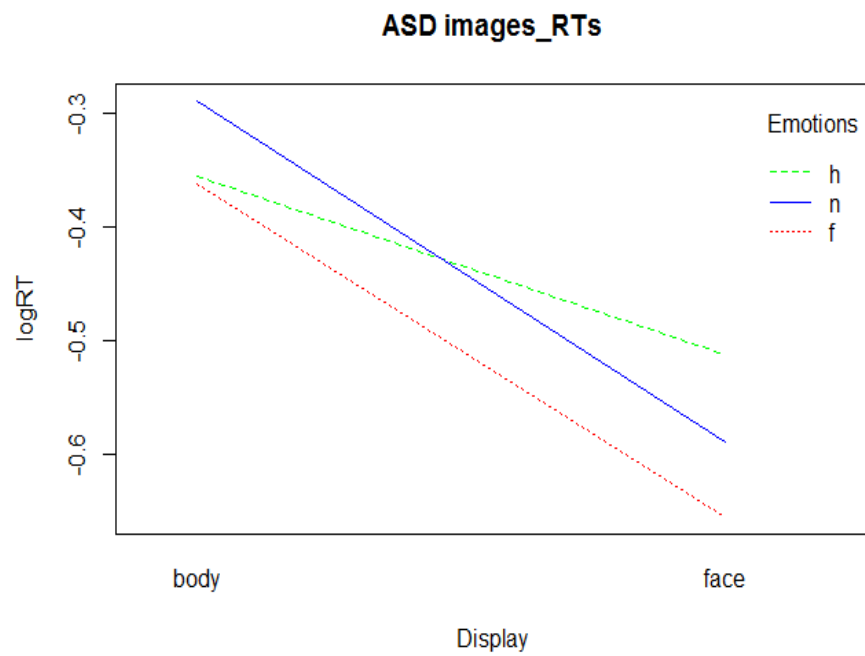
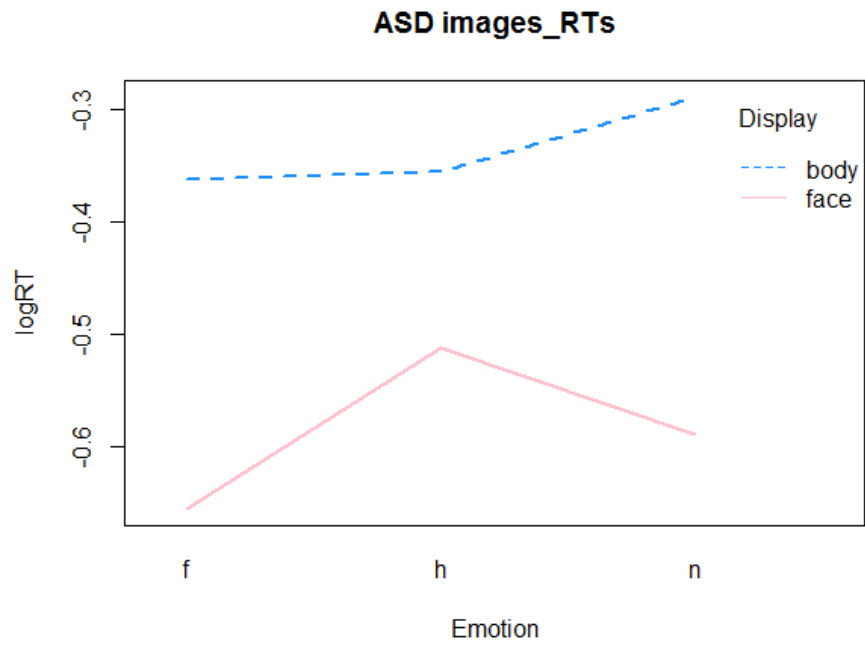


Figure 17. Representation of RTs relative to static stimuli recognition in participants with ASD.

Between group comparison: Within group comparison showed that the processing of emotional bodies and faces in participants with ASD is different from that of TD participants. But was the ASD's

performance impaired with respect to that of TD or simply different? To answer to this question, a 2x3x2 repeated measures ANOVA with display (face and body) and emotion as within factors, and group as between factor was performed. We found a main effect of display ($F_{(1,38)} = 15.964$, $p < .000$), showing that in both groups faces were recognized faster than bodies, and a significant effect the emotion ($F_{(2,76)} = 3.917$, $p = .024$). Post hoc comparison revealed that fearful stimuli were recognized significantly faster than happy ($p = .005$). However, the effect of group ($F_{(1,38)} = 0.100$, $p = .753$) was not significant, suggesting that the overall ability of people with HF ASD to recognize static images of facial and bodily expressions is not impaired but simply different. It is possible that to recognize the emotions from static images, individuals with ASD use different strategies from the ones adopted by TD individuals, however those alternative strategies seems to be equally effective. None of the interactions was not significant either (all $p > .05$).

Given the previous result suggesting an importance of the display, we further investigated the RTs of ASD and TD groups separately in the two classes of stimuli. A 3x2 ANOVAs with emotion as within factor and group as between factor was performed in each class of stimuli. The analysis of RTs relative to recognition of **Faces** showed a significant effect of emotion ($F_{(2,76)} = 3.889$, $p = .024$). Post hoc comparison showed that fearful faces were recognized faster than happy expressions ($p = .011$). The effect of **group** ($F_{(1,38)} = .030$, $p = .863$) and the interaction ($F_{(2,76)} = .111$; $p = .895$) were not significant.

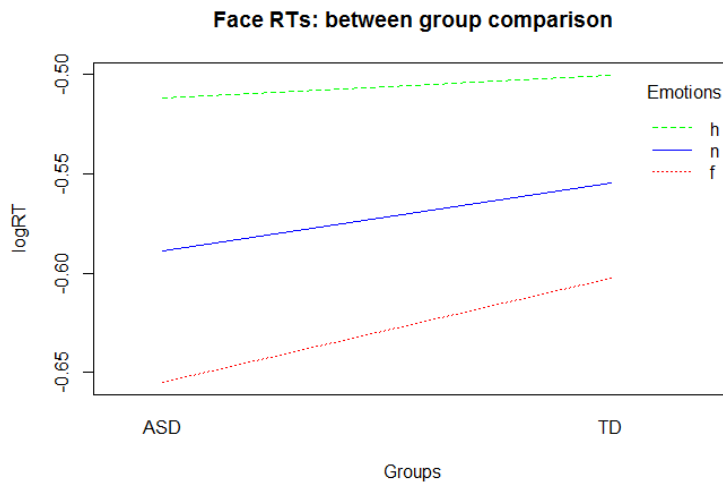
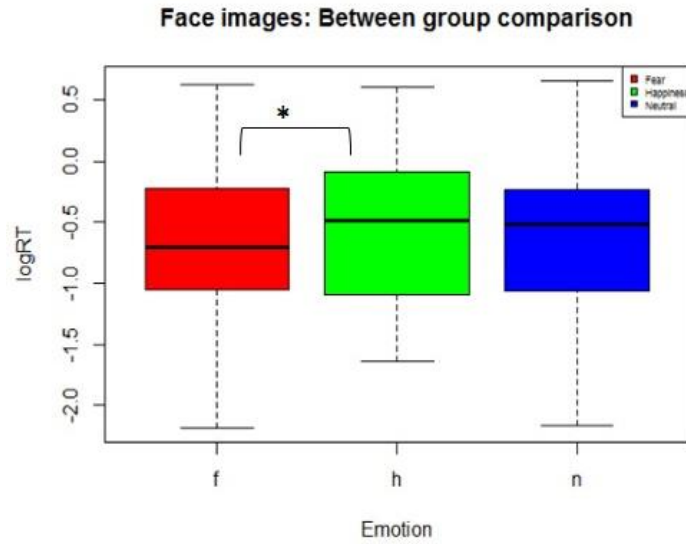


Figure 18. Representation of ANOVA's main effect of emotion in face (RTs). The top graph represents the main effect of emotion, with fearful faces recognized faster than happy. The bottom graph shows similar trend in the two groups across emotion, with no difference in rapidity between ASD and TD. Fear is represented in red, Happiness in green, and Neutral in blue. Significant results are represented with square brackets and asterisks. The empty circles represent outliers. In the top graph, the vertical lines represent the 1st and the 3rd quartile.

Analysis of RTs relative to **Body** stimuli showed no significant effects of group ($F_{(1,38)} = .833, p = .366$), emotion ($F_{(2,76)} = 2.55, p = .085$) or interaction ($F_{(2,76)} = .367, p = .694$). Qualitatively, the RTs were longer

in participants with ASD while fearful stimuli were recognized faster in both groups, however this differences did not reach statistical significance in ANOVA analysis.

Taken together, between group comparisons of static images suggested that individuals with ASD recognize facial expression with the same rapidity of TD participants, but they seems to need longer time for recognizing the emotional content of body pictures.

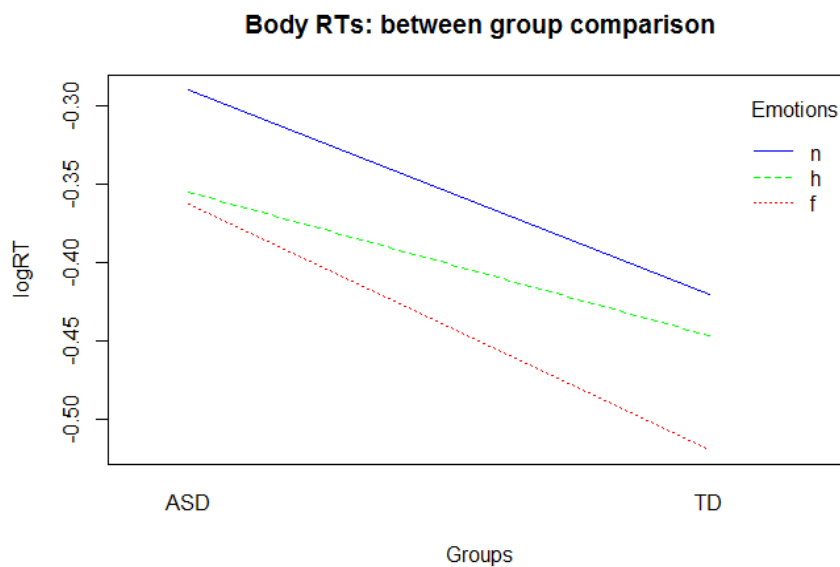
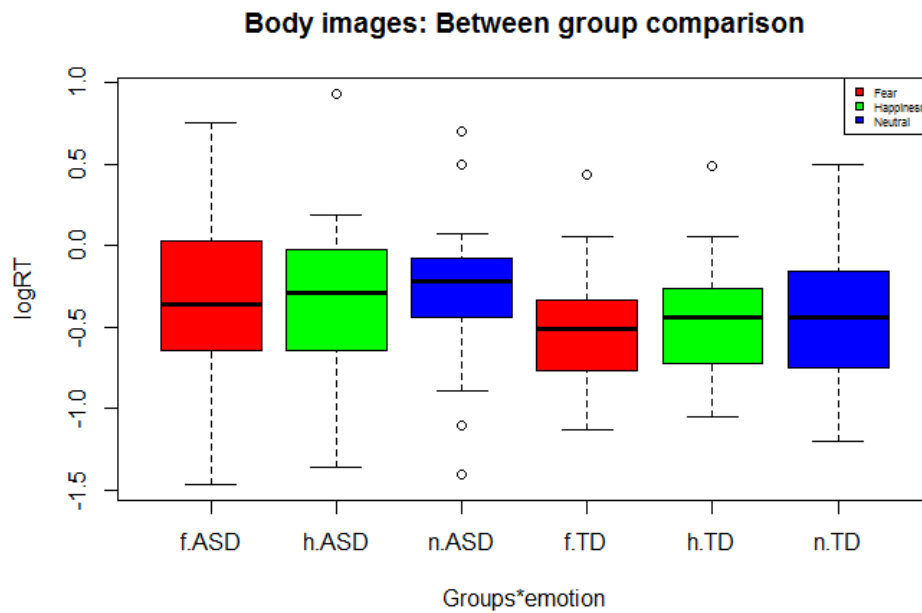


Figure 19. Representation of ANOVA's main effect of emotion in body images (RTs). No effect was significant. The top graph represents the RTs in the two groups in all the emotional contents. The bottom graph shows the RTs trend in the two groups across emotion, with any difference in rapidity between ASD and TD. Fear is represented in red, Happiness in green, and Neutral in blue. In the top graph, the vertical lines represent the 1st and the 3rd quartile. The empty circles represent outliers.

2.3.2.2. The second research question we wanted to investigate was whether the vision of the body form, compared to the sight of pure motion information, could influence the time needed to identify the emotional content of body movements. In another words: "Is there any difference in RTs between FLDs and PLDs"?

Within group comparison: AS we did for the images, we initially compared the RT relative to FLDs and PLDs separately in each group. A 2x3 repeated measures ANOVA with display (PLDs and FLDs) and emotion as within variables was performed.

ASD: results showed a significant main effect of display in ASD group ($F_{(1,19)} = 6.833, p = .017$), with FLDs recognized faster than PLDs. The effect of the emotion was not significant ($F_{(2,38)} = 1.425, p = .253$), either was the interaction ($F_{(2,38)} = .667, p = .519$).

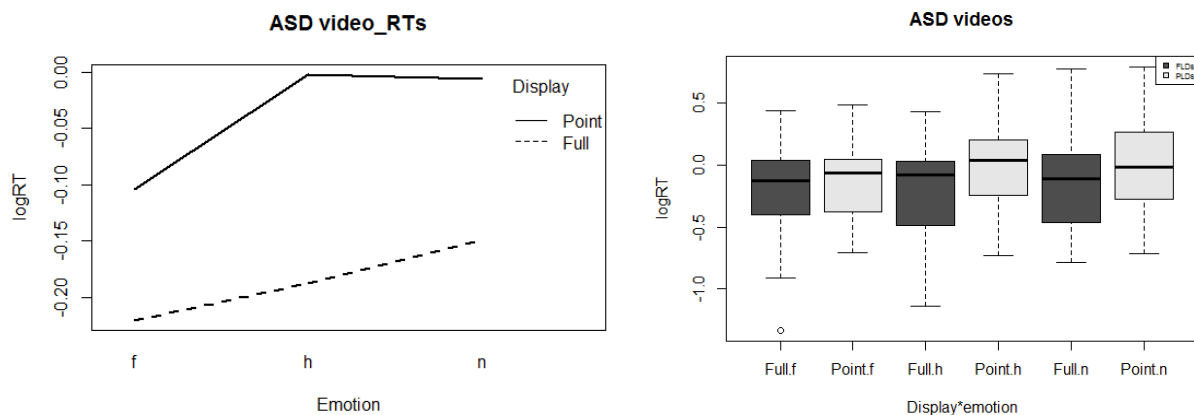


Figure 20. Representation of RTs across display in ASD, subdivided by emotions. PLDs are represented with solid line (left graph) or light grey boxplots (right graph) The graphs clearly show the main effect of display, with higher RTs in PLDs compared to FLDs. In the right graph, the vertical lines represent the 1st and the 3rd quartile.

TD: analysis in TD group showed similar results. We found a main effect of display ($F_{(1,19)} = 4.683, p = .043$), in particular TD participants recognized the FLDs faster than the PLDs. Nor the effect of emotion ($F_{(2,38)} = .928, p = .404$) nor the interaction ($F_{(2,38)} = 1.975, p = .152$) were significant.

Within analysis of RTs in videos suggested that individuals with ASD code the dynamic stimuli similarly to TD. But are people with ASD slower than TD in processing those stimuli? To answer this question we compared the RTs between the two groups.

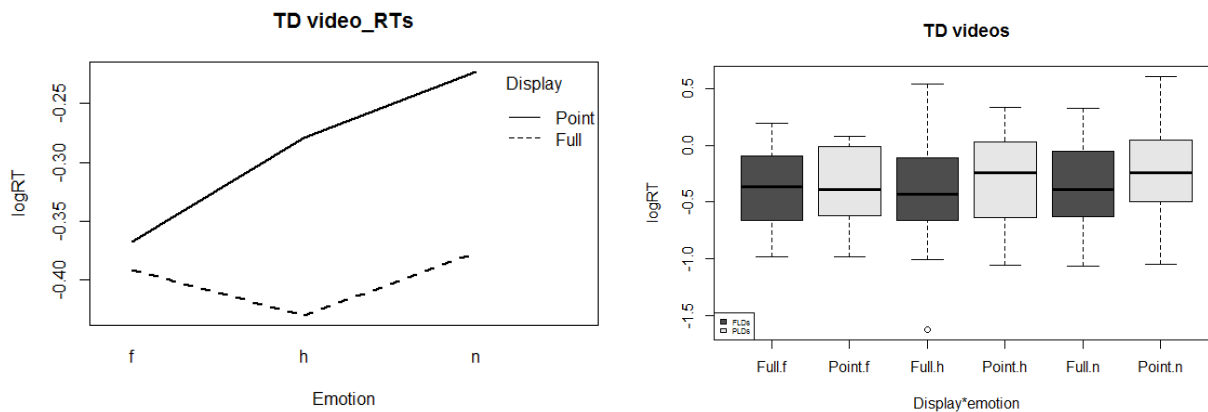


Figure 21. Representation of RTs across display in TD, subdivided by emotions. PLDs are represented with solid line (left graph) or light grey boxplots (right graph) The graphs clearly shows the main effect of display, with higher RTs in PLDs compared to FLDs. In the right graph, the vertical lines represent the 1st and the 3rd quartile.

Between group comparison: a 2x3x2 repeated measures ANOVA with RTs as dependent variable, display (FLDs and PLDs) and emotion as within variable, and group as between variable was performed.

Results showed a main effect of group ($F_{(1,38)} = 5.202, p = .028$) and a main effect of display ($F_{(1,38)} = 11.497, p < .002$). In particular, TD identified the emotional valence of dynamic body movements faster than ASD, and the FLDs were recognized with shorter RTs than the PLDs in both groups. The effect of the emotion ($F_{(2,76)} = 2.128, p = .126$) and all the interactions were not significant (all $p > .12$).

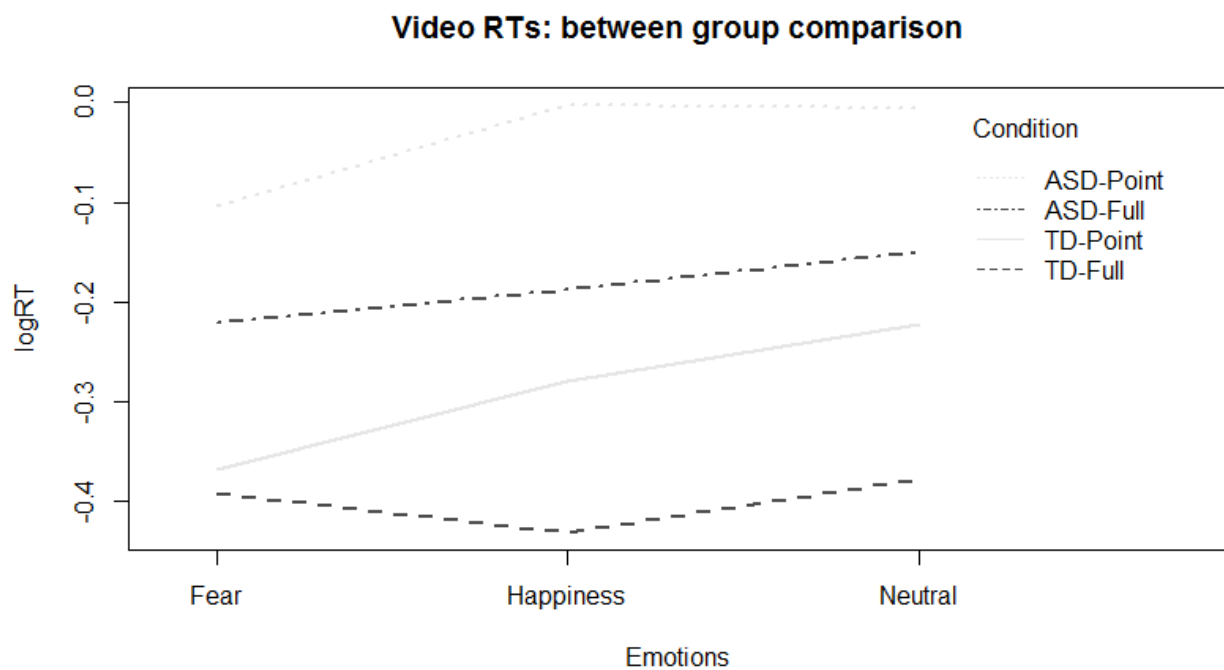


Figure 22. Representation of RTs relative to PLDs (light grey lines) and FLDs (dark grey lines), across emotions (x axis) in the two groups.

Furthermore, since the effect of display was significant, we investigated the differences between groups separately in FLDs and PLDs. Results of repeated measures ANOVAs in **PLDs** with emotion as within factor and group as between factor confirmed the **main effect of group** ($F_{(1,38)} = 5.826, p = .020$), with ASD responding slower than TD. Also, we found a main effect of emotion ($F_{(2,36)} = 3.665, p =$

= .030), while the interaction was not significant ($F_{(2,76)} = .219, p = .803$). Post hoc comparison revealed that fearful videos were recognized faster than neutral ($p = .037$) but not than happy ($p = .113$), and no differences emerged between happy and neutral videos either ($p = 1$). On the contrary, analysis in **FLDs** showed only a **marginal effect of group** ($F_{(1,38)} = 3.564, p = .066$), and no effect of emotion ($F_{(2,76)} = .618, p = .541$) or interaction ($F_{(2,76)} = .336, p = .716$).

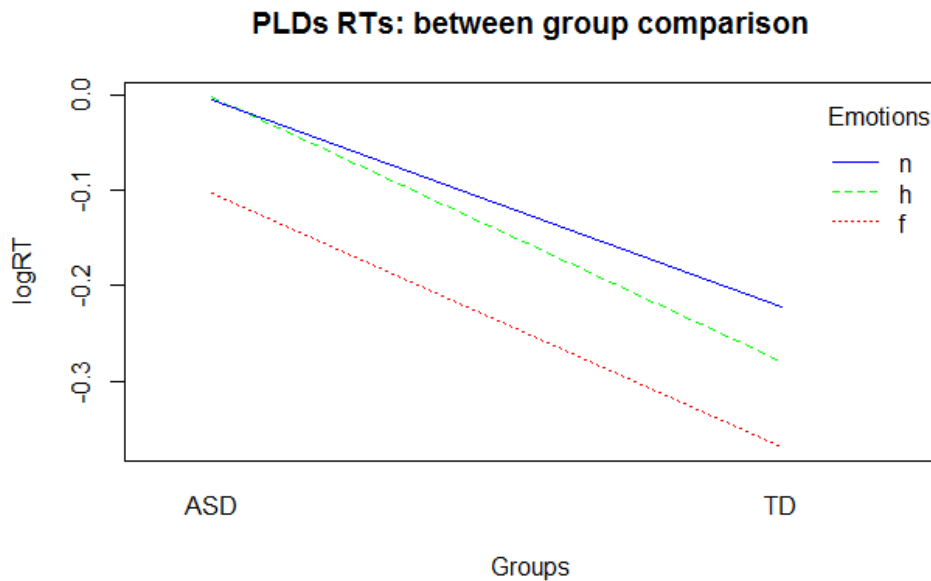


Figure 23. Representation of RTs in PLDs across emotions subdivided by groups. Fear is represented in red, Happiness in green, Neutral in blue.

2.3.2.3. Our third research question was whether there is a difference in recognizing the body expressions represented by dynamic or static stimuli. And also, is the perception of the actual movement important for better identify the different emotional meanings of body movements?

Within group analysis: As in the previous analysis, we initially explored the differences within each group, permuting 3x3 repeated measures ANOVAs with display (body, FLDs and PLDs) and emotion as within variables in the two groups separately.

ASD: Results in ASD showed a main effect of display ($F_{(2,38)} = 10.166$, $p > .000$), with body images recognized significantly faster than FLDs ($p = .003$) and PLDs ($p < .000$), and FLDs faster than PLDs ($p = .001$). On the contrary, the effect of emotion ($F_{(2,38)} = 2.043$, $p = .144$) and the interaction ($F_{(4,76)} = .548$, $p = .700$) were not significant.

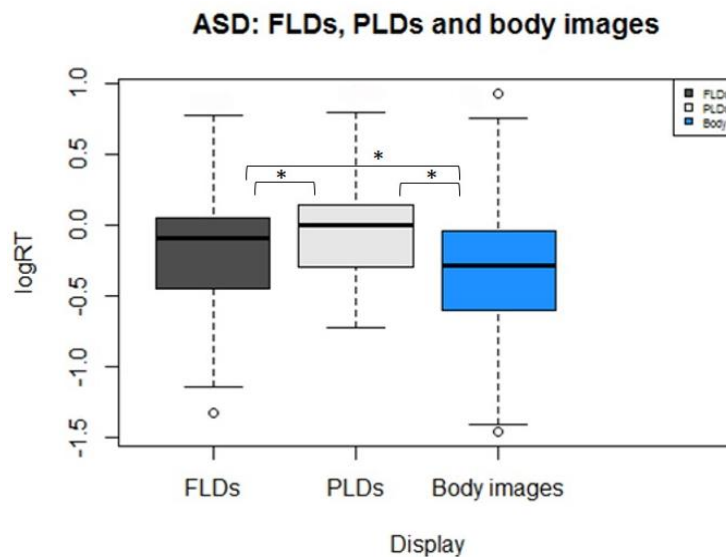


Figure 24. RTs in ASD, comparison between static body images (light blue) and dynamic body movements (FLDs in dark grey, PLDs in light grey). Significant results are represented with square brackets and asterisks. The empty circles represent outliers. The vertical lines represent the 1st and the 3rd quartile.

TD: Similar results were found also in TD group. The only significant result was the main effect of display ($F_{(2,38)} = 4.411$, $p = .019$). Post hoc comparisons showed higher RTs for PLDs with respect to FLDs ($p =$

.019) and bodies ($p = .002$), but the difference between body and FLDs was not significant ($p = .595$).

The effect of the emotion and the interaction were not significant ($F_{(2,38)} = 2.006$, $p = .148$ and $F_{(4, 76)} = .772$, $p = .547$ respectively) as well.

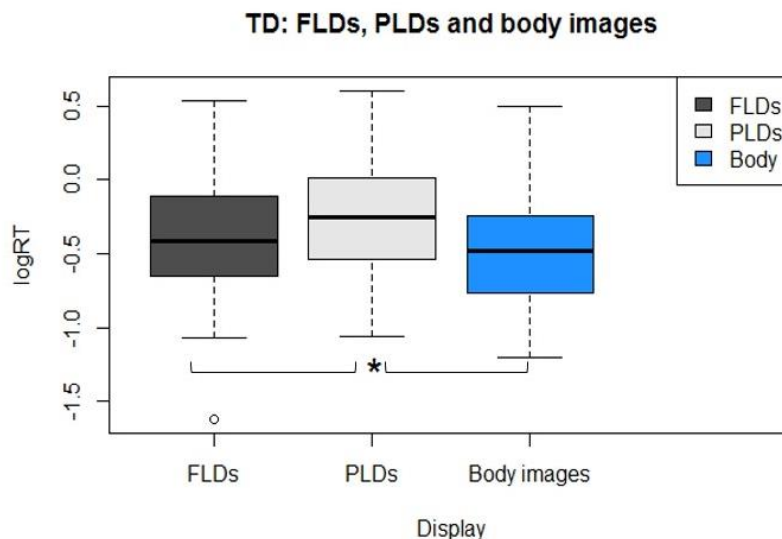


Figure 25. RTs in TD, comparison between static (light blue) and dynamic body stimuli (FLDs in dark grey; PLDs in light grey). Significant results are represented with square brackets and asterisks. The vertical lines represent the 1st and the 3rd quartile.

Between group comparison: a 3x3x2 repeated measures ANOVA with RTs as dependent variable was performed. Display (body, FLDs and PLDs) and emotion were used as within variables, and group as between factor. When the two groups were compared, results showed a main effect of display ($F_{(2,76)} = 14.192$, $p > .001$) and a main effect of emotion ($F_{(2,76)} = 4.028$, $p = .022$), while the effect of group was marginally not significant ($F_{(1,38)} = 3.34$, $p = .075$). Post hoc comparisons showed that the recognition of body images was quicker than that of PLDs ($p < .000$) but did not differ from FLDs ($p = .120$); also FLDs were recognized faster than PLDs ($p < .000$). Moreover, fearful stimuli were identified faster than neutral ($p = .002$) but not than happy ($p = .240$); finally happy movements were not different from neutral ($p = .415$).

2.4. Discussion

Despite decades of research on recognition of emotions with facial and bodily expression, scientific results in ASD are still contradictory (Harms et al., 2010; Kaiser & Shiffrar, 2009; Pavlova, 2012). Contradictory results may be due to several factors - such as IQ matching criteria, age, task demands and stimulus type (i.e. static or dynamic). Those factors might explain the variations in emotion recognition in individuals with ASD, especially within high-functioning subjects, as they can adopt different compensatory mechanisms according to the task and to the stimulus type (Actis-Gross et al., 2015). The aim of the present study was to investigate the ability of individuals with HF ASD in recognizing emotions across a range of different social signals – such as facial and bodily expression. Furthermore, among the body movement, we explored differences in understanding the emotional content represented by implied (images) or explicit (videos) motion. With regard to static stimuli, for images of face and body recognition we did not find any group difference in accuracy and RTs, in line with previous findings (Doody & Bull, 2013; Libero et al., 2014; Peterson, Slaughter, & Brownell, 2015; Weisberg et al., 2014). However, within group analysis revealed some differences in the two groups. In TD participants, accuracy and rapidity were similar between bodies and faces independently of the emotional valence, confirming that bodily expressions are equally good in conveying emotions than faces (de Gelder et al., 2010). This result suggests that the emotional significance is processed similarly for facial and bodily expressions in TD individuals, however this is in contrast with happy face and happy body advantage found by Actis-Grosso and collaborators (2015). A possible explanation for this difference could be due to the stimuli's time of presentation. In fact, in our experiment, facial stimuli lasted 3 seconds (this choice was made to maintain consistence in time of presentation between the different classes of stimuli), while in Actis-Grosso et al. the images of faces lasted 1 second. Therefore,

it is possible that the longer time of exposition might have prevented us to detect the variability in response time during emotional face recognition.

Results in HF ASD group were partially different. Similarly to TD, we found no differences in accuracy for facial expressions. On the contrary, participants with HF ASD recognized images of fearful bodies more accurately than happy and neutral body images. In addition, they were faster in recognizing expressions from faces than from bodies, especially fearful and neutral stimuli, suggesting a specific difficulty in ASD population in comprehending the meaning of body movements. Taken together, results on static images recognition suggest that HF ASD might use different - but equally successful - strategies to recognise the emotional meaning of pictures depicting bodily and facial expressions.

By contrast with static body images, we found an impairment in ASD group in recognizing the dynamic body stimuli (FLDs and PLDs). In fact, despite no group differences in accuracy, participants with ASD were slower than TD in identifying the emotional content of PLDs and (marginally) of FLDs. This result suggest that when the motion information are just implied – as in body images – HF ASD can correctly infer the emotional meaning of body expressions. On the contrary, they have difficulties in encoding cues from explicit motion – as is in the video clips of FLDs and PLDs. This finding is in line with previous studies (Atkinson, 2009; Nackaerts et al., 2012; Philip et al., 2010) and confirms the results of our experiments described in Chapter 1, suggesting that individuals with ASD struggle in processing the information conveyed by dynamic body movements.

When the emotional content is considered, our results suggest that happiness is better conveyed by faces, while its identification results challenging when conveyed by bodies. On the contrary, fear seems to be easier recognisable when is expressed by body gestures. This seems to be true for both groups. In fact, we found that both TD and HF ASD recognized the happy faces with higher accuracy than all the

other happy stimuli. Furthermore, participants with HF ASD recognized happy faces more rapidly than happy PLDs and FLDs. These results are in line with previous researches on facial recognition (for a meta analysis see Nummenmaa & Calvo, 2015), and confirm the existence of a happy face advantage also in individuals with HF ASD (Farran, Branson, & King, 2011; Actis-Grosso et al., 2015). In addition, our results show that happiness is scarcely understandable from body movements. In fact, movements displaying happiness were understood worse than the other body expressions. Moreover, comparing emotions within the display we found that TD participants identified happy PLDs less accurately than fearful and neutral PLDs; and happy FLDs worse than neutral FLDs. Similarly, participants with HF ASD recognise happy body images less accurately than fearful ones; and happy FLDs worse than fearful FLDs. Those results suggest that the body motion is not the more efficient channel to convey joy. This could be explained accordingly to what I have already hypothesised in Chapter 1. That is, happy expressions indicate the presence of something pleasant and it is plausible that happy signals are more useful when they are close to the observer, as they are more easily reachable and sharable. When we are close to someone, faces are the prioritized source of information, while bodies are crucial to communicate messages from a distance. For this reason, happy faces are reasonably a better candidate than bodies in conveying happiness. However, our result seems to be in contrast with the happy body advantage found by Actis-Grosso et al. (2015) using emotional PLDs. One possible explanation for this different findings could be due to the different variety of the set of stimuli. In fact, in our experiment we presented 10 different videos for each emotional category (10 happy, 10 fearful and 10 neutral PLDs), while Actis-Grosso et al. used only 4 stimuli per emotional condition. The variety of PLDs included in our set of stimuli was greater, our stimuli was more numerous and they probably included also less intense or less prototypical happy body movements, which might be less clearly recognizable than he

ones adopted in Actis-Grosso et al. (2015). Another reason that might account for the different results could be ascribed to the task. In fact, we asked to participants to perform a 2 option forced-choice task, while Actis-Grosso et al. adopted a 4 option forced-choice task. In our experiment participants performed an easier task, as they were asked to distinguish fear (negative emotion) from one positive (happiness) or one neutral options. On the contrary, the task in Actis-Grosso et al. included one option corresponding to a positive emotion (happiness), but three options corresponding to emotions with negative valence (fear, anger and sadness). Therefore, it is plausible that to distinguish between similarly negative emotions is more confusing and might have disadvantaged the recognition of fear, while the recognition of the only positive emotion (happiness) was facilitated. As a consequence, this disparity in the option choice's emotional valence could have been reflected in a lower accuracy for fear and higher accuracy for happiness.

With regards to fearful stimuli, we found no display differences in TD, nor in accuracy nor in RTs. By contrast, fearful content seems to facilitate individuals with HF ASD in recognizing both dynamic and static stimuli. With regards to static stimuli, fearful faces were identified faster than the other fearful stimuli. As reported before, happy faces were recognized better in HF ASD. However it seems that when the emotional content is correctly identified, fearful faces are encoded faster. Furthermore, images of fearful bodies were identified more accurately than happy and neutral body images. With regards to dynamic stimuli, participants with HF ASD recognized fearful and neutral FLDs better than happy FLDs. Altogether, those results showed that in individuals with HF ASD the body movements are more easily recognized when they express fear. Therefore, our findings suggest that in individuals with HF ASD the emotion of fear is processed more efficiently than the other emotional content. These outcomes are in

contrast with some previous studies which posited a deficit in encoding fearful signals in HF ASD, possibly related to dysfunctions in amygdala (Ashwin, Chapman, Colle, & Baron-Cohen, 2006b; Hadjikhani et al., 2009; Howard et al., 2000; Schultz, 2005). However, as I have suggested in Chapter 1, the body is the best candidate in conveying fearful signals because it can be seen from a distance, and thus it allows the observer to activate adaptive responses in time. Therefore, to our opinion, it is not completely surprising that stimuli with so high survival impact – such as the fearful bodies - are better recognized than movements with different emotional valence, also in individuals with HF ASD. It is important to remember that our sample includes people with high cognitive level, who have likely developed compensatory mechanisms that might enable them to comprehend social relevant stimuli, especially when evolutionary vital. As abovementioned, the recognition of dynamic movements is impaired in this population. Albeit a general difficulty-frame, the stimuli better comprehended are the one crucial for survival, to wit the fearful body signals. In addition, the vision of a fearful face could be even more salient than a frightened body, as it imply that something scaring is not far from the observer. Due to the proximity, the reaction need to be extremely rapid. This could explain why the scared faces are processed faster than body stimuli.

Going back to our between group comparisons, they showed that individuals with ASD recognized facial expression and body movements with the same accuracy and rapidity than TD participants. This could suggest that they are able to correctly infer the significance of the emotional expressions from static stimuli at TD level. However, there could be another explanation as we might have critically missed some differences because of the experimental procedure. In fact, to maintain coherence across the types of stimuli, we presented the images for 3 seconds, that is quite a long time of exposure, especially

for perceiving images. It is possible that participants had recognised the static stimuli in less than 3 seconds, but in our paradigm they could not respond before the images disappeared. This could be the reason why we did not find any group difference in RTs and accuracy between conditions in images. Also, it is likely that TD had recognized the stimuli faster than ASD, but we constrained participants to wait by 3 seconds and therefore we might have missed this difference. Furthermore, thanks to this long presentation participants with ASD had enough time to correctly elaborate the emotional valence of presented stimuli. But it could be possible that a shorter presentation of the stimuli might cause a drop of the accuracy. We will investigate those possibilities in future studies. Additionally, it is worth noticing that adolescents and adults who participated in the present study have been in treatment in our laboratory for years. Often, intervention with ASD includes materials as pictures and emotion identification training. Therefore, it is possible that they have compensate previous difficulties in understanding emotional information, or simply that they have practice with images recognition and are skilled in identifying this kind of stimuli. The images we used clearly represented the emotions and their expression was mostly exaggerated, therefore easily recognizable. Moreover, in the present study participants were asked to perform a not requesting experimental task. In fact, it has been showed that participants with ASD have also difficulties in maintaining attention and in working memory (Barendse et al., 2013; Happé, Ronald, & Plomin, 2006). When the task is complex the performance of participants with ASD might be worsen by this complexity. Therefore, results might reflect not only the difficulties specific of the investigated domain, but also difficulties task-related. For this reason, to minimize the cognitive resource request by the task we decided to present only three emotional contents. Critically, we tested individuals with high level of intelligence. Thus, there is the possibility that we obtained a ceiling effect in the accuracy because the task was actually too simple for them. To unmask difficulties

in identifying the emotional expression from static images in this treated population with high cognitive resources, it might be of help i) to use more subtle expression, ii) to present the stimuli briefly and iii) to use more complex task, such as increasing the number of emotions presented or the choice options. In future studies we will address those different possibilities.

Images-criticality aside, our results evidenced a deficit in understanding dynamic body stimuli in individuals with ASD. This findings has noteworthy implications for treatment. People with ASD might find challenging to make eye contact or to confront faces at close distance (Tanaka & Sung, 2016). But reading the body language could be less troublesome than reading the facial expressions. In fact, body movements can be viewed at “safer” interpersonal distance than faces, far from the possibility that the person being watched will react or expect social reciprocity. Therefore, body language might be a more congenial channel for perceiving emotions. For this reason, besides focusing on facial expression, interventions with ASD should train also the ability to pay attention at the body as possible source of social relevant information. The correct interpretation of body movement might help individuals with ASD to better infer feelings and intentions of other people. In turn, an improved comprehension of others will be reflected in amelioration of social exchanges. In a virtuous circle logic, the experience of positive interactions might reinforce the sense of social-efficacy, which in turn favours new social situation seeking. And the more frequent and copious are the expositions to social signals, the broader are the opportunity that individuals with ASD have to test the acquired skills and to train the weaker ones. Thus, learning how to interpret the information conveyed by body movements might enable people with ASD to reduce their social awkwardness.

Chapter 3

MOTION OR E-MOTION? REPRESENTATION OF OBSERVED EMOTIONAL BODILY EXPRESSIONS IN THE ANTERIOR INTRAPARIETAL CORTEX AND SUPERIOR TEMPORAL SULCUS: A TMS STATE-DEPENDENT STUDY

Abstract

Autism Spectrum Disorder (ASD) is characterized by difficulties in social interaction (American Psychiatric Association, 2013). People with ASD are impaired in recognizing human movements, both neutral and emotional. Thus, it is not clear if social difficulties are related to a specific deficit in emotion recognition, or due to a general impairment in human motion perception. We tried to disentangle this issue by using the TMS adaptation paradigm. Adaptation is a phenomenon in which changes in neural tuning and excitability induced by prolonged exposure to sensory stimulation can bias the perception of the stimuli subsequently presented. TMS stimulation reverse this effect.

In a behavioural study, we first explore the existence of a neural system specialized for the elaboration of emotional body movements. Participant were adapted with point-light video clips depicting fearful, happy or neutral actions and then asked to recognize point-light with same/different emotional content. Results showed an adaptation aftereffect only for incongruent stimuli, suggesting the existence of a neural mechanism for perceiving the body emotion specifically. Subsequently, in a TMS experiment we explore the possible location of this mechanism. The sites we stimulated are nodes of the neural network responsible for the human motion understanding, and they are reported to be abnormally activated in ASD. We found a reversed after-effect following TMS over aIPS, while the adaptation was still present after stimulation over pSTS and the control site. These results demonstrate

that aIPS contains neurons that specifically code for the emotional body expressions, suggesting that the difficulties encountered by individuals with ASD in understanding the emotional signal during social interaction might rely to deficit in this mirror area.

3.1. Introduction

The human being is an extremely social animal and action understanding is crucial for juggling in everyday life. Perception of biological motion - like the movements of the eyes, face, body parts or entire body - conveys social meaning and is crucial for social interaction (Allison, Puce, & McCarthy, 2000; Clarke et al., 2005). Detecting prey or predators, identifying pleasant or dangerous situations, learning new skills and inferring social norms are just some examples that clearly illustrate the fundamental importance of comprehending our conspecifics' movements. In the visual field, the elaboration of whole body human gestures has traditionally been studied with the so called point-light display (PLDs) (Johansson, 1973) paradigm, also referred to as biological motion (BM) stimuli. These stimuli portray an actor performing whole-body actions, represented as a few illuminated dots moving over a black background. The dots are placed over the major joints and the head, thus the facial expression is never visible. This offers the great advantage to isolate motion signals from others visual cues, hence all the information that can be inferred from these stimuli is purely conveyed by the human movement. In healthy subjects, the perception of PLDs is sufficient to infer a large amount of social information, such as actor's identity (Troje et al., 2005), gender (Kozlowski & Cutting, 1977), type of action performed (Dittrich, 1993; Johansson, 1973; Norman, Payton, Long, & Hawkes, 2004) and emotional content (Alaerts et al., 2011; Atkinson et al., 2004, 2007, 2012; Chouchourelou et al., 2006; Clarke et al., 2005; Dittrich et al., 1996). In humans, a widespread network of interconnected brain

areas (known as the action observation system- AOS) underlies the comprehension of conspecifics' body movement, including the superior temporal sulcus (STS), particularly its posterior part (Blake & Shiffrar, 2007; Puce & Perrett, 2003), and both frontal and parietal nodes of the putative "mirror neurons" system (MNS) (for a review, see (Cattaneo & Rizzolatti, 2009) The brain areas of the AOS code for different aspects of the body movement. For instance, STS contains the visual representation of the actions performed by other individuals, both in monkeys' (Jellema, Maassen, & Perrett, 2004; Perrett et al., 1989) and in humans' brain (Allison et al., 2000; Puce & Perrett, 2003; Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009). Its neurons encode for the observed human movements without generalizing to the actions' goals (Jellema et al., 2004; Perrett et al., 1989)). The MNS, on the other hand, is implicated in higher-order processing of multisensory information for motor execution and comprehension. The MNS has originally been discovered in area F5 in the macaque brain (di Pellegrino et al, 1992), corresponding to area BA 44-46 in humans. Subsequently, neurons with mirror properties have been described also in monkey's anterior intraparietal cortex (AIP) (Ferrari et al., 2005), which corresponds with the superior parietal sulcus in the human brain (Grafton et al. 1996a, see Rizzolatti et al. 2014 for a review). Its neurons respond both to the performance and to the observation of actions (Rizzolatti & Craighero, 2004) In particular, the parietal node of the MNS is responsible for encoding the higher-order goal representation of performed (Tunik, Rice, Hamilton, & Grafton, 2007) and observed (Cattaneo, Sandrini, & Schwarzbach, 2010; A. F. d. C. Hamilton & Grafton, 2006) motor acts. These findings are in favor of the concept of a common system representing both one's own and other's actions, supporting the proposed role of motor system as a "direct-matching" between self and others crucial for the comprehension of other people's feelings, intentions and beliefs (Vittorio Gallese et al., 2004; Iacoboni et al., 1999).

The importance of correctly understand the body movement is clearly evidenced by the last two decades of findings in clinical populations with deficits in social interaction, such as the Autism Spectrum Disorder (ASD). The ASD is a neurodevelopmental disorder characterized by “Persistent deficits in social communication and social interaction across multiple contexts”, “Deficits in social-emotional reciprocity” and “Deficits in nonverbal communicative behaviours used for social interaction” (American Psychiatric Association, 2013). Alteration of both STS and fronto-parietal mirror areas have been proposed as explanations for ASD difficulties in understanding other people’s movements. At the behavioural level, difficulties in biological motion perception have been widely reported in ASD (Kaiser & Pelphrey, 2012). Accordingly, neuroimaging studies have showed altered structural, functional and connectivity patterns in pSTS regions in the brain of individuals with ASD (Alaerts et al., 2014; Freitag et al., 2008; Kaiser & Pelphrey, 2012). In particular, when the task involves emotion processing (e.g. reporting the emotional state of PLDs) ASD-specific deficiencies have been reported consistently (Alaerts et al., 2014; Atkinson, 2009; Hubert et al., 2007; Nackaerts et al., 2012; Parron et al., 2008). In addition, the involvement of the right intraparietal sulcus (IPS) in ASD has been shown in several brain imaging studies, even during the processing of non-emotional stimuli. For example, a PET study showed a negative correlation between the qualitative impairment in social interaction and the activation in the right parietal region (Gendry Meresse et al., 2005). This result was confirmed by some fMRI studies using BM neutral stimuli (Freitag et al., 2008), showing a negative correlation between bilateral IPS activation during a BM recognition task and social interaction and communication score in ASD and, furthermore, a reduced grey matter volume in right IPS in individuals with ASD. In another study comparing ASD and control groups, McKay and colleagues (McKay et al., 2012) found that the activation in the inferior parietal lobule (IPL) during the perception of walking PLDs

was specific for TD participants. Coherently, Oberman and Ramachandran (Oberman & Ramachandran, 2007) suggest that in the ASD brain the visual information about human movement is integrated in the temporal areas, but it is not transmitted from there to the associative parietal cortex. This might result in a more difficult - or less efficient - internal simulation of the observed action, which may underlie some of the social impairment.

Although neuroimaging studies can reveal which brain regions are active during BM perception, this kind of evidence does not permit any inference about the causal role of the cortical areas involved in BM processing. In contrast, studies in patients with brain-lesion and brain stimulation paradigms in healthy individuals do help to unveil substrates responsible for biological motion perception. For instance, neuropsychological studies reported impaired perception of human PLDs in patients with parietal lesion (Battelli, Cavanagh, & Thornton, 2003; Schenk & Zihl, 1997; Vaina & Gross, 2004), suggesting that this area is involved in the elaboration of biological motion information.

To date, only two TMS studies have explored the causal role of pSTS in perceiving BM (Grossman, Battelli, & Pascual-Leone, 2005; van Kemenade, Muggleton, Walsh, & Saygin, 2012). Both these findings confirmed the importance of pSTS for BM detection by using PLDs depicting neutral action embedded in noise. So far, the causal role of pSTS in elaborating the emotional body expressions has never been investigated.

Besides, a recent TMS study (Engelen, de Graaf, Sack, & de Gelder, 2015) provided causal evidence that IPL is involved in emotional body processing, showing that on-line TMS over IPL selectively affected the recognition of fearful bodies. However, the role of STS was not considered in this study. Furthermore, the authors used the TMS “virtual lesion” approach, which generally causes a behavioural impairment, though they found an improvement when stimulating IPL. Although using TMS as a “virtual lesion”

method offers the advantage to study the causal role of specific brain areas by reversibly perturbing selected cortical regions in healthy individuals (Cowey, 2005; Walsh & Pascual-Leone, 2003), this technique has more recently been criticized as too simplistic and it has been pointed out that its precise physiological effects still need further specification (Allen, Pasley, Duong, & Freeman, 2007; Miniussi, Ruzzoli, & Walsh, 2010; Juha Silvanto, Muggleton, & Walsh, 2008). For instance, TMS can induce a wide range of behavioural and perceptual effects depending on the initial activation state of the stimulated region (J Silvanto, 2008). The TMS adaptation paradigm (J Silvanto, 2008), partially overcomes these limits. Adaptation is a well-known phenomenon based on the trial-by-trial reduction of a physiological response to repeated stimuli (Gibson & Radner, 1937). A prolonged exposure to sensory stimulation induces changes in neural tuning of neurons that code for the presented stimulus. Neurons encoding the adapted attribute are made less active by adaptation, and this produces a biased perception of subsequently presented novel stimuli (Grill-Spector, Henson, & Martin, 2006; Mather, Verstraten, & Anstis, 1998). In the TMS adaptation paradigm, the initial state of the cortex is manipulated by perceptual adaptation to a particular class of stimuli. The adapting stimulus induces habituation in a subset of cells that code for particular stimulus features, making them a selective target for TMS modulation. The adaptation phenomenon clearly shows how the neural impact of an external stimulus is state-dependent, that means it is not only determined by the properties of the perceived stimulus, but also on the susceptibility of the stimulated brain region to be activated by the stimulus. Accordingly, also the effects of TMS stimulation are state-dependent, because TMS selectively facilitates the less active neural populations. It has been shown that stimulation time-locked to the cognitive task, delivered over the cortical area containing the adapted neurons, selectively improves processing of the adapted stimulus in the domain of vision (Guzman-Lopez et al., 2011; Juha Silvanto et al., 2008),

language (Sato et al., 2011), and motor control (Cattaneo et al., 2010). These findings demonstrate that the TMS adaptation paradigm offers the opportunity to explore the role of functionally distinct but spatially overlapping neural populations within the stimulated region. For this reason, in our experiment we adopted the TMS adaptation paradigm (J Silvano, 2008) to investigate the contribution of pSTS and aIPS in encoding whole body movements with different emotional valence.

This causal approach is of particular interest to better understand neuropsychiatric conditions that show clear deficits in social domains and interpersonal communication, such as Autism Spectrum Disorders (ASD). As I said before, the mirror neuron system has been claimed to be involved in empathy and comprehension of other people's feelings (Rizzolatti & Fabbri-Destro, 2010), pSTS has been described as the key node for social interaction (Kaiser & Shiffrar, 2009; Pavlova, 2012) and abnormalities in these network have been used to explain the difficulties that people with ASD encounter in social interaction. However, most studies employed tasks or stimuli without any explicit social meaning. Therefore it is not clear whether these areas contain neurons that code for emotions or whether they are broadly activated by the sight of human actions. Previous studies have shown the importance of pSTS and aIPS during perception of neutral movements, but what happens when the observed movement is an emotional expression? Disentangling this issue may help to clarify the origin of the impaired understanding of emotional body expressions in people with ASD. In the present experiment we used the TMS state-dependent paradigm to investigate the existence of neurons coding specifically for emotional body movements within aIPS and pSTS. Previous studies indicate that the right pSTS region is more active than the left pSTS during BM perception (Bonda, Ostry, & Evans, 1996; Grossman et al., 2000; Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004; Pelphrey, Morris, & McCarthy, 2004). Also, the STS region has been reported to be ipsilaterally interconnected with aIPS

both in monkeys (Seltzer & Pandya, 1994) and in humans (Arfeller et al., 2013). Hence, we decided to stimulate pSTS and aIPS both in the right hemisphere. We initially adapted participants to PLDs depicting fearful or happy movements. We then asked them to recognize emotionally congruent or incongruent PLDs, while we applied TMS to either aIPs, pSTS or an occipital control site. If the stimulated area contains neurons coding for the emotional meaning of the body movement, we expect to find an adaptation after-effect with emotional PLDs, with TMS facilitating the recognition of the adapted emotion. On the contrary, if these areas are responsible for coding the movement in general, irrespective of its emotional content, we should not find any aftereffect and thus no TMS-induced behavioural facilitation. If TMS over aIPS, pSTS, or both, results in a reversed after-effect of adaptation for emotional body movements, this means that those areas contain neurons coding specifically for the emotional content of human body movement. As aforesaid, previous findings had shown the causal role of those area in encoding neutral movements. Consequently, we could hypothesize that the abnormal functioning of those areas could account for both deficits in emotion and in motion comprehension in ASD population. On the contrary, if the after-effect of adaptation is not modulated by TMS it means that in the stimulated brain area there is no neural population coding specifically for emotional content of whole body expressions. The confirmation of the latter hypothesis would suggest that the impairment in emotion understanding in ASD might not - or at least not primarily – be related to those areas.

3.2. Methods

3.2.1. Stimuli: we used a total of 30 point-light display (PLDs), out of which 10 stimuli depicted emotional positive (happy), 10 stimuli depicted emotional negative (fearful), and 10 stimuli depicted

emotionally neutral whole-body movements. These stimuli are part of a wider dataset originally created by Atkinson et al. (Atkinson et al., 2004) and subsequently modified by Atkinson et al. (Atkinson et al., 2012) . We selected happy and fearful actions because both are emotionally highly arousing, but have opposite emotional valence. To create the stimuli, five females and five males between 18 and 22 years old were recruited from the final year undergraduate classes in Drama or Performing Arts at King Alfred's College in Winchester, and were instructed to spontaneously perform emotional and neutral actions. The PLDs consisted of 2 second-long digitalized and Matlab-transformed video clips (see Atkinson et al. 2012 for details), displaying a single actor represented as 13 white dot-lights moving on a black background. The dots were positioned over the head and the main joints of the actor (one dot over each ankle, knee, hip, elbow, shoulder, and hand). The neutral stimuli reproduced 10 different common human movements without emotional content, and included: 1 walking on the spot, 2 hopping, 2 digging, 1 knocking, 1 star-jumping and 3 bending to touch toes. The emotional stimuli represent 10 different expressions of Happiness and 10 different expressions of Fear, portrayed with different intensity and different movements. Examples of the stimuli can be viewed at <http://community.dur.ac.uk/a.p.atkinson/Stimuli.html>.

3.2.1.1. Pilot experiment: Since the actions represented in the PLDs stimuli were all different one from one another, we ran a pilot study prior to the TMS experiment to control for recognizability of the stimuli, emotional intensity and quantity of movement contained in every stimulus.

Participants: 16 healthy adults (13 females, age mean= 29.63 , age SD= 7.65) were presented with a total of 30 stimuli (10 PLDs depicting Fear, 10 Happiness and 10 neutral actions). Participants of the pilot study were students at the University of Westminster in London or friends of them. All

participants volunteered and signed an informed consent before starting the experiment, according to the Declaration of Helsinki.

Procedure: Participants were tested individually in a quiet room. They seated in front of 24-inch monitor, located approximately at 60 centimetres from the observer. All the stimuli were presented at the centre of the screen. The experimental procedure (stimuli presentation and responses registration) was implemented with the software E-Prime 2.0[®]. For each clip, participants were first asked to recognize the emotion expressed by the actor by pressing the corresponding button on the keyboard, then to rate the “Intensity of the emotion” and the “Quantity of movement” using a scale from 1 to 5. Participants could choose between 4 options: the three emotional categories, plus the option “Other”. This latter option was included in case participants did not recognize the observed emotion as one of the three proposed options. With the option “Other” they were not forced to select one option just because it was the “least wrong”, and this allowed us to evaluate the real level of recognizability of each stimulus category. The response options were randomized across participants, they were indicated with a label placed over the keys “F,G,H,J” and the options were also always presented below the stimulus on the PC monitor. The rating was done using the numeric keys on the top of the keyboard.

Pilot results: the percentage of correct categorizations over the total number of presentations was calculated for each video (Accuracy). Also, the rated intensity of the emotion and the rated quantity of movement were averaged for each video (Intensity and Movement, respectively). The data distribution was tested for normality with a Shapiro test, and since the results were significant we adopted a non-parametric test for further analysis. Accuracy, Intensity and Movement were compared between the three emotional categories using a Wilcoxon signed rank test with continuity correction, and the p-

value was adjusted with Bonferroni correction. Results did not show any significant differences between the three emotions either for Accuracy (all p-values > 0.1), or Movement (all p-values > 0.05). With regard to the Intensity, we did not find any differences between Fear and Happiness ($V = 26$, p-value = 0.9187), but predictably the Neutral actions were judged as less intense than Fear ($p = 0.006$) and Happiness ($p = 0.006$). The absence of differences between the emotions ensure that the future results could not be attributed to differences in recognisability between the emotional categories, intensity of the expressed emotion or quantity of movement contained in the stimuli.

3.2.2. Behavioural Experiment

To our knowledge, there are no studies showing an adaptation effect specific for emotional PLDs. Hence, we first run a behavioural study to investigate the existence of a mechanism in the human brain specifically coding for the emotional body movement. Using the adaptation paradigm, we measured RTs during the recognition of emotionally congruent and incongruent PLDs.

3.2.2.1. Behavioural Participants: 26 healthy adults (14 females, age mean = 23.58 years; age SD = 2.95 years) took part in the behavioural study. All participants volunteered, they were recruited in Rovereto and were students at the University of Trento or friends of them. All participants had normal or corrected-to-normal vision. The study has been approved by the local ethical committee, in accordance with the Declaration of Helsinki. Before undergoing the experiment, all participants received an exhaustive explanation of the experimental procedure and provided written informed consent.

3.2.2.2. Behavioural Procedure: Participants seated in a comfortable chair in front of a 24-inch computer screen at a distance of around 60 cm. Participant were presented with 18 trials consisting of 1 minute adapting period, followed by a series of 8 probe trials. Every trial began with a white central fixation cross over a black background lasting for 10 seconds. The adapter stimuli consisted in a total of 18 different 2-seconds point-light displays, representing 6 happy, 6 fearful and 6 neutral whole-body movements, so that half of the test stimuli were emotionally congruent and half were incongruent with the adapter. During the adaptation part, the same video was repeated 30 times, and participants were asked to simply watch the stimuli and focus over the emotion expressed by the actor. At the end of the adaptation part, a prompt slide appeared, asking participant to “get ready for the task”. Then, a total of 8 test stimuli (4 bodily expression of Fear and 4 of Happiness) were presented in a random order. For each test stimulus, participant were asked to categorize the expressed emotion by key-press as fast as possible. E-Prime version 2.0 (Psychology Software Tools, Inc.) software was used for stimulus presentation and response recordings. The movie clip was presented centrally, the question “Which emotion?” appeared on the above part of the screen, and the two response options (“Fear” and “Happiness”) were presented on the bottom part of the monitor. If participants took longer than 2 seconds to recognize the emotion (i.e. longer than the stimulus duration), the movie disappeared while the question and the response options lasted until participants responded. The response options were indicated with a label placed over the keys “G” and “H”, and the key-emotion correspondence was randomized across participants. Participants were asked to respond using the index and the middle finger of their right hand. Accuracy and response time (RT) were recorded. To avoid temporal summation of triple-pulse TMS stimulation, the inter stimulus interval (ISI) was set to 5 seconds. Since

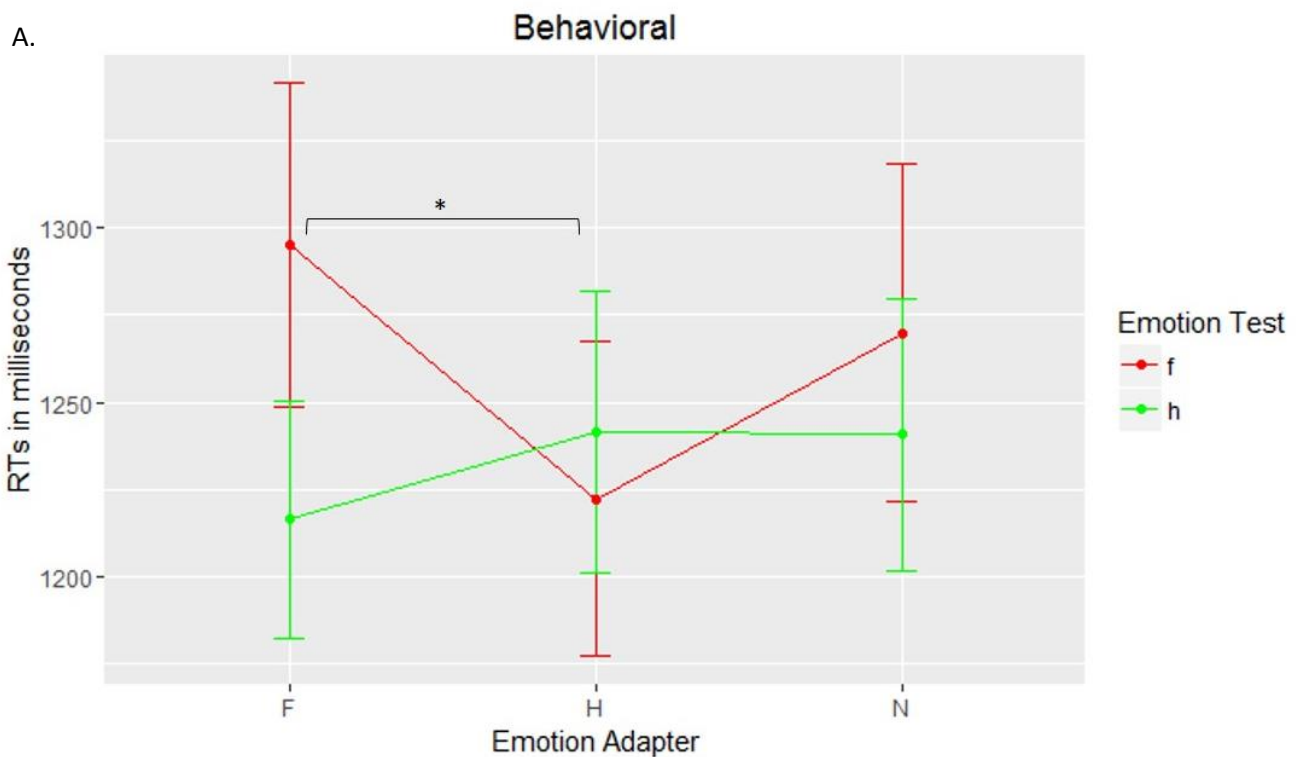
the after effect decreases over time, to better control for this decay we kept the ISI fixed by presenting a black slide lasting for 5 sec minus the participant's RT.

3.2.2.3. Behavioural Analysis: The analyses were performed with the software package R, version 3.3.1. The dependent variable in this experiment is the response time (RT). Only the stimuli correctly recognized were considered in the analysis. The outliers were determined for each participant in each stimulation site using the 1.5xIQR criterion¹. Data distributions were tested for normality with a Shapiro test and the homoscedasticity of variances was assessed with a Bartlett test. To normalise the data, the RT were log-transformed before the subsequent analysis. A repeated measures ANOVA with the emotional content of the adapter (emoAdapt: Fear/Happiness) and probe stimuli (emoTest: Fear/Happiness) as within-subject factors was performed on the averaged logRT. Post hoc comparisons were performed with a 2-tailed T-test for paired samples separately in every stimulation site and the resulting p-values were Bonferroni corrected.

3.2.2.4. Behavioural Results: The ANOVA showed no main effect of emoTest ($F_{(2, 25)} = 2.14, p = .156$) or emoAdapt ($F_{(2, 50)} = 1.62, p = .207$), but the interaction between the two factors was significant ($F_{(2, 50)} = 8.47, p < .001$). To disentangle the interaction, we split the data according to the emotional class of test stimuli and in each of them we compared the logRT between the three adapter emotional categories. We found that when participants were asked to recognize fearful stimuli, the RTs were significantly

¹ The 1.5xIQR criterion is more conservative than the 3xIQR criterion that we have adopted in the previous experiments (described in Chapter 1 and 2). As explained in page 27, we adopted a less conservative criterion in the studies involving participants with ASD in order to include in the analysis the maximum number of possible observations and to maximize the power of the analysis. Especially in participants with LF ASD, the percentage of errors was higher than in TD group, and the response times were highly variable. Therefore, a conservative criterion to detect the outliers would have excluded a sizable number of items, decreasing the power of the analysis. On the contrary, in the present experiment participants were all TD individuals, the variance of their responses was more homogeneous and the number of the outliers was much smaller. A more conservative criterion (the 1.5xIQR criterion) is more sensitive and more effective to detect the outliers in a more homogeneous distribution, as the distribution of RTs in TD participants was. For these reasons, in the present experiment we adopted the 1.5xIQR criterion instead of the 3xIQR criterion.

higher for adapter Fear (i.e. emotionally congruent) compared with adapter Happy (i.e. emotionally incongruent) ($p = .007$), but there was no difference between adapter Fear and Neutral ($p = .394$). On the contrary, when the test stimuli was Happy the logRT did not change significantly according to the emotional category of the adapter stimuli previously presented: the difference between the adapter Happy and Fear, and between the adapter Happy and the Neutral were not significant ($p = .52$ and $p = 1$ respectively). Since the neutral adapter did not affect the RT neither when the test stimuli displayed happiness nor fear, we did not include it in further analyses. We collapsed together the RTs for happy and fearful test stimuli according to their congruence with the previous adapter and we subsequently compared congruent with incongruent stimuli. We found significantly higher logRT when the adapter's and the test's emotional category coincided ($t = 3.29$, $df = 25$, $p = .003$), that is an adaptation after-effect.



B.

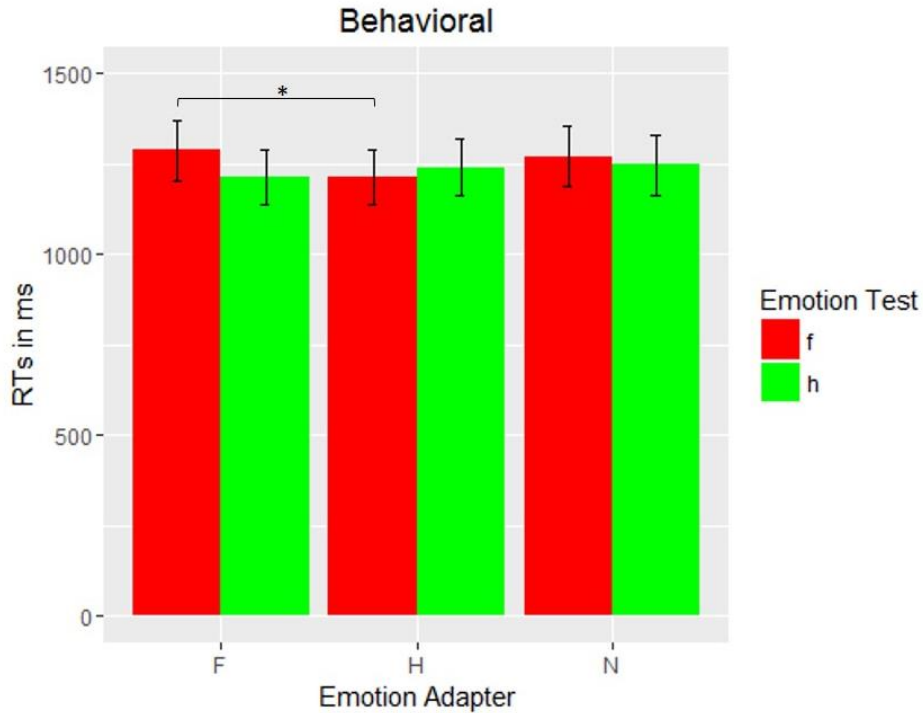


Figure 26. The y axis represents the response times (RTs) in milliseconds in the behavioral experiment. The x axis shows the emotion of the adapter stimuli (F is for Fear, H is for Happiness, N in for neutral). In figure A. the lines represent the test stimuli; the dots represents the mean of RTs; the vertical bars represent the standard error. In figure B. the mean RTs by the test stimuli are represented in the columns of the histogram; the black vertical bars represent the standard error. In both the graphs, fearful stimuli are represented in red, happy stimuli are represented in green. Significant results are represented with square brackets and stars.

3.2.3. TMS Experiment: The behavioural results provide the first evidence for the existence of an adaptation after-effect for emotional content of whole-body PLDs. With the TMS study we aimed to investigate the neural substrate underlying this mechanism. The TMS experiment consisted of two different parts: MRI acquisition and TMS stimulation. The two parts were administered on two different days.

3.2.3.1. TMS Participant: 17 healthy adults (11 females, age mean= 25.63 years; age SD= 5.17) participated in the TMS experiment. Participants were recruited at the University of Westminster in London and received a £ 15 voucher refund for their participation in the present experiment. All

participants were right handed and had normal or corrected to normal vision. The study was approved by the local ethical committee, in accordance with the Declaration of Helsinki. Before the start of the experiment, all participants received an exhaustive explanation of the experimental procedure, they were screened for fMRI and TMS contraindication and provided written informed consent.

3.2.3.1. TMS settings and procedure: The three different sites (pSTS, aIPS and the control site) were stimulated on the same day, with 30 minutes of delay between the three sessions. The order of stimulation sites was counterbalanced between participants. Participants wore earplugs and were seated in a comfortable chair in a quiet room, in front of a 24-inch computer screen at a distance of 60 cm, with their head on a chin-rest. For each stimulation site, participants were presented with 12 blocks which started with a 1 minute adapting period, followed by a series of 8 probe trials, leading to a total of 96 test stimuli for each stimulation site. We decided to not present the Neutral adapter, because in the behavioural study we found that RTs for Neutral adapters did not differ from RTs when the adapter and test stimulus were emotionally congruent. Therefore, the TMS procedure was exactly identical with that of behavioural experiment, apart from the fact that we only presented emotional stimuli. The test stimuli could be emotionally congruent (i.e. conveying the same emotional information) or emotional incongruent (i.e. conveying different emotional information) from the adapters. The E-Prime version 2.0 (Psychology Software Tools, Inc.) software was used for stimulus presentation, response recordings, and for the triggering of the TMS pulses.

3.2.3.2. Neuronavigation: For each participant, a high resolution T1-weighted MPRAGE scans (176 partitions, 1 x 1 x 1 mm, flip angle = 7°, TI = 1,000 ms, TE = 3.57 ms, TR = 8.4 ms) was acquired before the TMS experiment to allow MRI-neuronavigated positioning of the coil over the stimulation sites.

Structural MRI images were obtained with a 1.5 T whole-body TIM Avanto System (Siemens Healthcare), at the Birkbeck/University College London Centre for Neuroimaging (BUCNI), with 32-channel head coil. For each participant a 3D reconstruction of the gray matter surfaces and the scalp were created using the Mesh morphing tool included in the TMS Neuronavigator software package (Brain Innovation BV, The Netherlands). To position the coil over the site of stimulation the 3D scalp reconstruction was coregistered with the actual participant's head. The same procedure was used to control for the coil position throughout the entire duration of the experiment.

3.2.3.3. Identification of stimulation sites: In each participant, three different sites in the right hemisphere were stimulated: the posterior part of the superior temporal sulcus (pSTS), the anterior part of the intraparietal sulcus (aIPS) and a visual posterior control area located over the midline. The three spots were identified on the basis of macro-anatomical landmarks. Specifically, the cortex around STS was targeted over its posterior portion, corresponding to the beginning of its posterior ascending branch in the parietal lobe. We defined the aIPS as the most rostral part of the IPS at the intersection between the postcentral gyrus and the IPS (Rice et al. 2006; Cattaneo, Sandrini, & Schwarzbach, 2010). The control site corresponded to a secondary visual area not primarily implied in coding for emotional aspect of visual stimuli, located between BA 17-19.

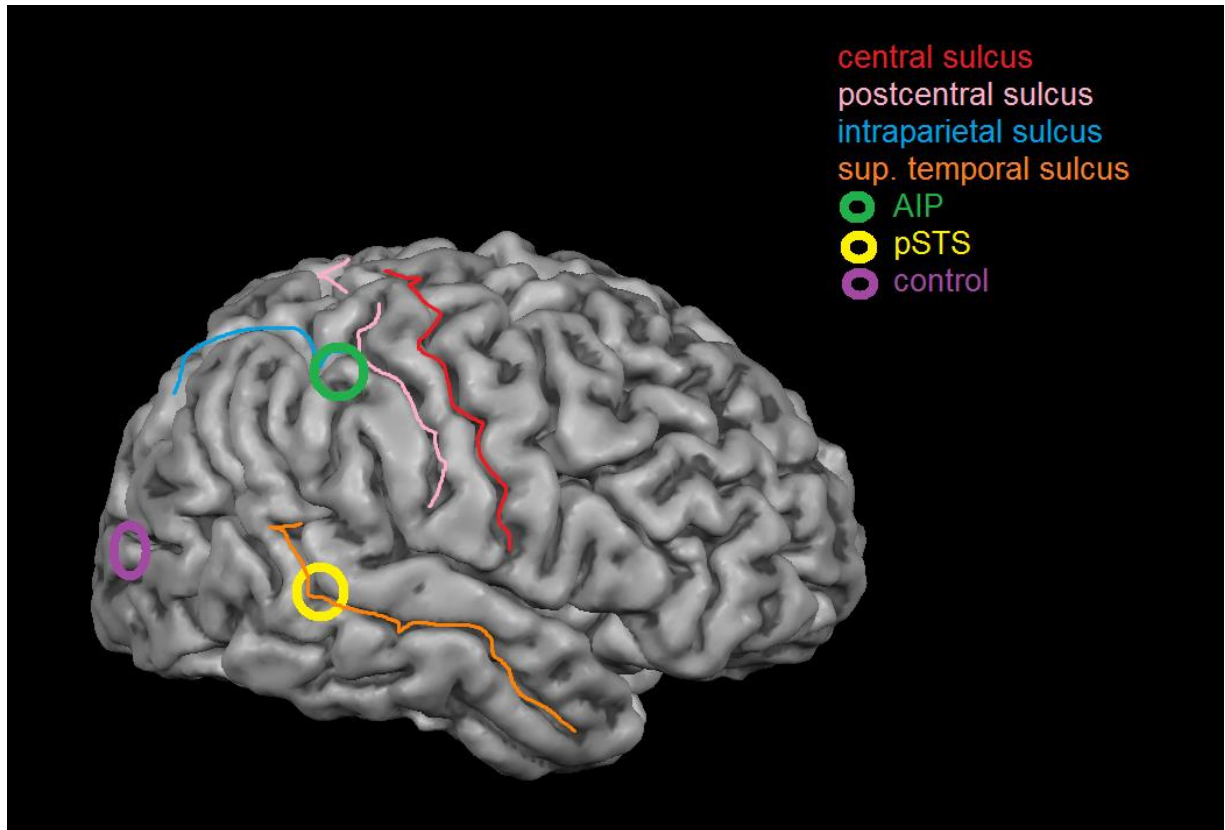


Figure 27. Cortical location of the stimulated brain areas

3.2.3.4. Transcranial Magnetic Stimulation: TMS pulses were applied with a figure-of-eight coil (D70mm coil) connected with a Magstim Rapid2 stimulator (Magstim Co Ltd, Whitland, UK). At the onset of each stimulus, participant received three 10Hz pulses. The intensity of the stimulation was set to 120% of the individual's resting motor threshold (rMT) with a maximum of 65% maximal stimulator output due to coil overheating. rMT is defined as the minimum TMS intensity sufficient to produce a visible motor-evoked response in the contralateral relaxed muscle (commonly the first dorsal interosseus – FDI) in at least 5 of 10 trials (Rossini et al, 1994), and was determined for each participant before the beginning of the experiment. The magnetic stimulator was triggered by E-prime software (Psychology Software Tools, Inc.). The coil was attached to a Magstim coil stand and placed tangentially

on to the skull. Coil orientation was anteroposterior with the handle pointing backward and slightly posteriorly (20 degrees from the mid-sagittal axis) for the aIPS position, in order to induce a posterolateral–anteromedial current in the underlying cortical tissue. For the stimulation of pSTS, the coil was positioned vertical with the handle pointing upward. Due to pSTS proximity to the ears, in some participants the coil orientation was changed to minimize the discomfort or to improve the contact of the TMS coil with the scalp. For the control site stimulation, the coil was positioned perpendicular to the midline with the handle pointing outward.

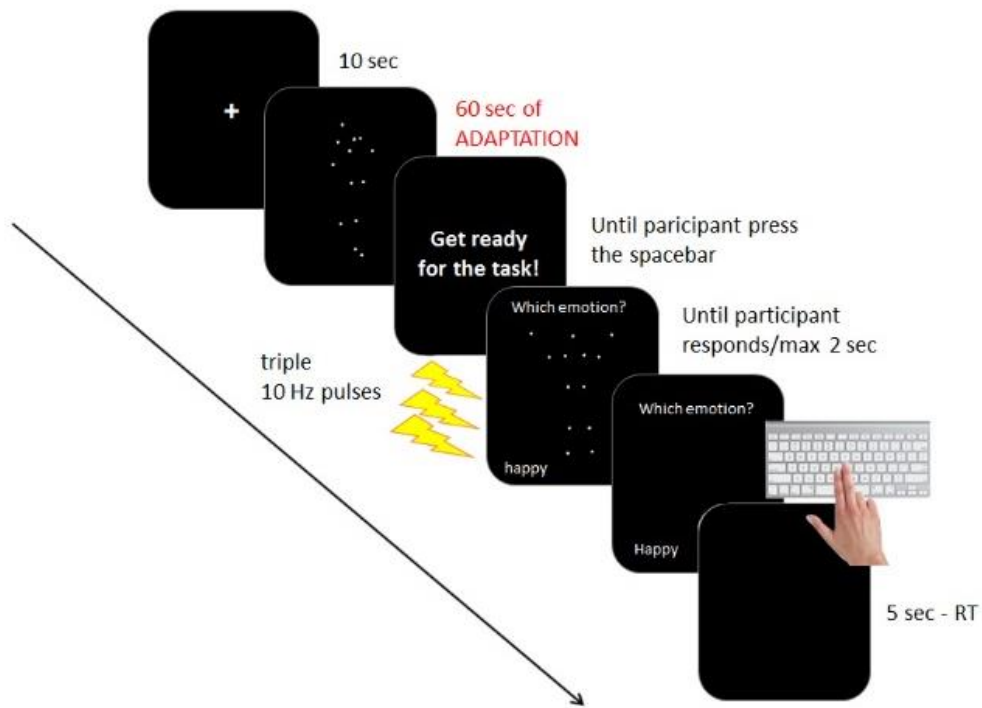


Figure 28. TMS Procedure timeline

3.2.3.5. TMS Analysis:

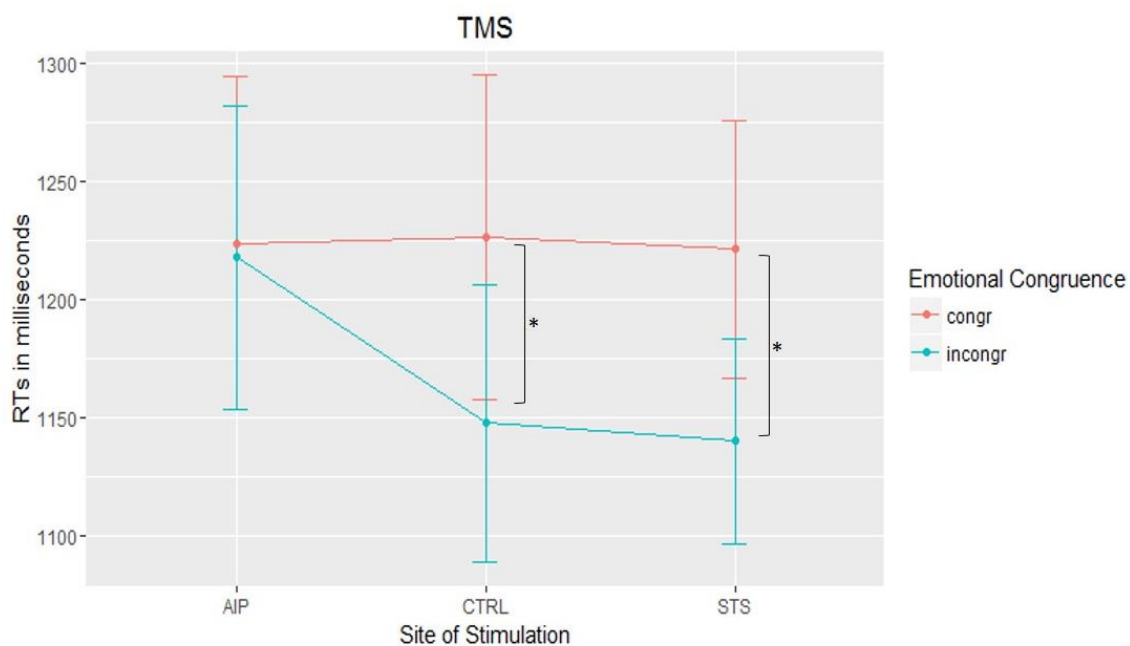
The analysis were performed with the R software package version 3.3.1. As for the behavioural study, the dependent variable is response time (RT) and only the correctly recognized stimuli were included in the analysis. The outliers were calculated for each participant in each stimulation site using the

1.5xIQR criterion and the RT below or above the obtained values were removed. In total, the percentage of removed outliers is 2.84%, and the number of removed outliers was similar between the two emotional content of probe stimuli (60 were fearful and 58 were happy stimuli). Two participants were excluded from the analysis because of the impossibility to find their rest motor threshold. In these participants, the TMS stimulation over M1 did not produce any visible hand twitch, and no motor sensation was perceived by them. Therefore, the final analysis were performed with a total of 15 participants. Repeated measure ANOVAs were performed on the logRT. The site of stimulation (“stimSite”) and the emotional valence of the adapter and probe stimuli (“congruence”) were considered as within factors. This latter factor considered the adapter-test emotional congruence, in terms of same (e.g. Adapter: fear – Test: fear) or different (e.g. Adapter: fear – Test: happiness) emotional content. According to that, the “congruence” is a factor with two levels: congruent and incongruent. To normalise the data, the RT were log transformed before the subsequent analysis. Data distribution were controlled for normality with Shapiro test ($W = 0.983$, $p\text{-value} = 0.317$) and the homoscedasticity of variances was assessed with Bartlett test for congruence (Bartlett's K-squared = 0.067, $df = 1$, $p\text{-value} = 0.795$); and stimSite (Bartlett's K-squared = 2.4901, $df = 2$, $p\text{-value} = 0.2879$). Post hoc comparison was performed with 2 tails pairwise t-test for paired data and results were adjusted with Bonferroni's correction.

3.2.3.6. TMS Results:

We initially performed an overall analysis excluding the outliers. A 2x3 repeated measures ANOVA with congruence, and stimSite as within factors was performed on the logRT. Results showed a significant main effect of congruence ($F_{(1,14)} = 15.645$, $p = .001$), with congruent stimuli recognized slower than

incongruent (mean RTs: congruent = 1223.83; incongruent = 1168.41), suggesting the presence of an adaptation effect and confirming the results of the behavioural experiment. However, it was not possible to exclude that the longer response time - determining the outliers - could be due to the stimulation itself, which we hypothesized having different effect in the three stimulation sites. Therefore, by excluding the outliers there was the risk to neglect the effect of the stimulation in one, or all, the sites of stimulation. For this reason, we performed another 2x3 repeated measures ANOVA including also the outliers in the analysis. Result confirmed the effect of the congruence ($F_{(1,14)} = 18.296$, $p = .0008$), and in addition it revealed a significant interaction between congruence and stimSite ($F_{(2,28)} = 3.798$, $p = .035$). Post Hoc comparison showed that in the control site and in pSTS the congruent stimuli were recognized faster than the incongruent ones ($p = .015$, and $p = .014$, respectively), suggesting an adaptation effect that was not modulated by the TMS stimulation. On the contrary, in aIPS the difference between the response times in recognizing congruent and incongruent stimuli was not significant ($p > .05$), suggesting that the TMS stimulation reversed the adaptation effect.



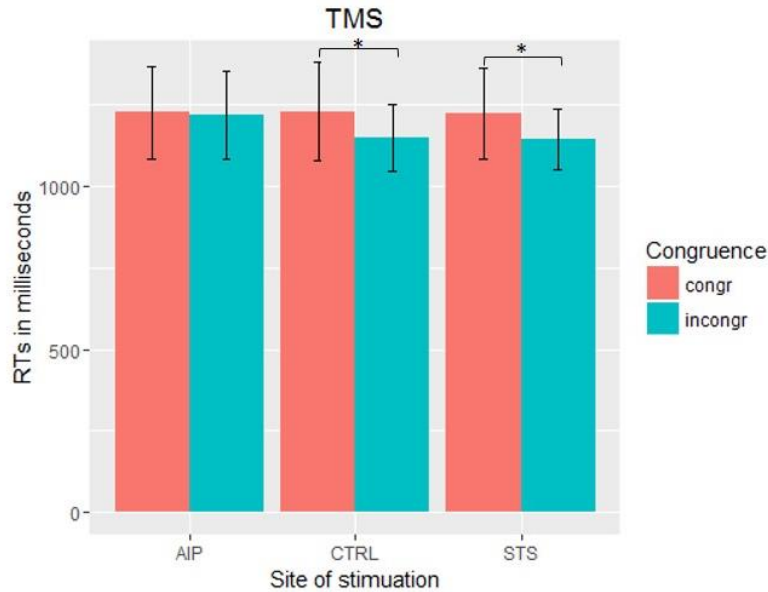


Figure 29. The y axis represents the response times (RTs) in milliseconds in the TMS experiment. The x axis shows the sites of stimulation. In figure A, the lines represent the congruence between the emotional content of test and adapters stimuli; the dots represents the mean of RTs; the vertical bars represent the standard error. In figure B, the mean RTs by the congruence are represented in the columns of the histogram; the black vertical bars represent the standard error. In both the graphs, congruent stimuli are represented in red, incongruent stimuli are represented in blue. Significant results are represented with square brackets and stars.

We further explored this results comparing the **magnitude of the adaptation effect** between the three stimulation sites. To this aim, in each participants we calculated the difference between the RTs in congruent and incongruent condition (“delta”). Subsequently, we performed a repeated measure ANOVA with delta as dependent variable and stimSites as within factors. Results showed a significant main effect of stimSite ($F_{(2,28)} = 3.798$, $p = .035$). Post hoc comparison revealed that the magnitude of the adaptation effect in aIPS was significantly smaller than the magnitude of the adaptation effect in the control site ($p = .035$) and in pSTS ($p = .022$), while there was no difference in the magnitude of the

effect between the control site and pSTS ($p = .922$). However, it must be acknowledged that these differences resulted significant only when the results were not corrected by the number of comparisons. By applying the Bonferroni's correction, the significance of differences between aIPS and the other sites partially decreased ($p = .066$, and $p = .105$, respectively with pSTS and the control site).

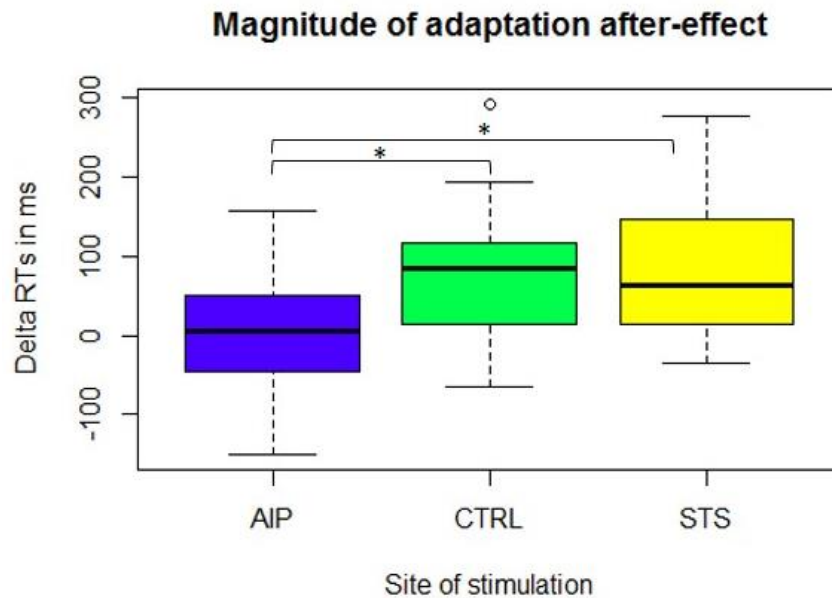


Figure 30. Comparison of the magnitude of the adaptation after -effect (delta) between the three stimulation sites. The vertical bars represent the 1° and 3° interquartile, the black line is the median. The empty circle represent outliers. Significant results are represented with square brackets and asterisks.

The results of the aforementioned analysis suggested that the TMS stimulation produced different effects in the three sites. Therefore, with the attempt to better understand it, we investigated this effect performing 2x2 ANOVAs in the three sites independently, with the emotional content of the probe stimuli (emoTest) and the emotional content of the adapter stimuli (emoAdapt) as separated within factors. Results both in the control site and in pSTS showed no significant effect for emoAdapt (CTRL: $F(1,14) = 0.355$, $p = .561$; pSTS: $F(1,14) = 2.164$, $p = .163$) and emoTest (CTRL: $F(1,14) = 0.703$, $p =$

.416; pSTS: $F_{(1,14)} = 1.403$, $p = .256$). On the contrary, the interaction between the two factors resulted significant (CTRL: $F_{(1,14)} = 6.668$, $p = .022$; pSTS: $F_{(1,14)} = 13.605$, $p = .002$), with incongruent stimuli recognized faster than congruent ones (i.e. an adaptation effect). In contrast, in aIPS neither the interaction ($F_{(1,14)} = 1.651$, $p = .219$) nor the main effects (emoAdapt: $F_{(1,14)} = 1.958$; $p = .183$; emoTest $F_{(1,14)} = 0.211$; $p = 0.653$) resulted significant, suggesting once more time that the TMS stimulation over aIPS reversed the adaptation after-effect. To dispel any doubt, the same analysis were also performed on the dataset including the outliers, which replicated the similar results with even higher significances (see table 6).

	aIPS				CTRL				pSTS			
	OUTLIERS		NO OUTLIERS		OUTLIERS		NO OUTLIERS		OUTLIERS		NO OUTLIERS	
	F	pvalue	F	pvalue	F	pvalue	F	pvalue	F	pvalue	F	pvalue
emoTest	0.516	.484	0.211	.653	<u>0.618</u>	<u>.445</u>	<u>0.703</u>	<u>.416</u>	<u>1.403</u>	<u>.256</u>	<u>1.403</u>	<u>.256</u>
emoAdapt	4.609	.049	1.958	.183	<u>0.216</u>	<u>.649</u>	<u>0.355</u>	<u>.561</u>	<u>2.164</u>	<u>.163</u>	<u>2.164</u>	<u>.163</u>
emoTest*emoAdapt	0.334	0.572	1.651	.219	11.858	.004	6.668	.022	13.605	.002	13.605	.002

Table 6. The table shows the results of the ANOVAs performed in the three stimulation sites separately, both considering and excluding the outliers.

3.3. Discussion

The goal of our experiment was to investigate the existence of neurons that specifically encode the emotional expressions conveyed by whole body movements. For the first time, our results clearly showed an adaptation after-effect following a prolonged exposure to emotional, but not to neutral PLDs. In particular, results of the behavioural experiment demonstrated that the explicit recognition of

emotional PLDs was slower when the emotional category of test and adapter stimuli were congruent, suggesting that neurons specifically assigned to the elaboration of the bodily expressions are present in the human brain. Starting from this striking evidence, we aimed to investigate the possible locus of the brain region underlying this effect. To this purpose, we used TMS adaptation paradigm asking participants to recognize congruent or incongruent emotional body expressions. We targeted two areas which are part of the action representation system: the anterior intraparietal sulcus (aIPS) and the posterior part of the Superior Temporal Sulcus (pSTS), plus a posterior visual region as control area. Our hypothesis was that if the stimulated brain regions contain neurons coding for emotional body expression, TMS should be more effective over the adapted neural population and reverse the adaptation after-effect. We found that the adaptation after-effect was still present following TMS stimulation over the control site and pSTS, replicating and confirming the existence of the adaptation after-effect that we found in our behavioural experiment. Furthermore, our results showed a reduced adaptation after-effect after TMS over aIPS. Since TMS is more effective when the neural activity is weaker, our findings suggest that aIPS contains neurons whose responsiveness decrease after a prolonged exposure to emotional PLDs – i.e. they are adapted by emotional PLDs – and thus they are more sensitive to TMS stimulation.

3.3.1. Interpretation of results in pSTS

Because impairments in social cognition represent a core ASD deficit, examining brain areas commonly involved in social processes can provide important insights into the mechanisms underlying this deficient domain (Pelphrey et al., 2011; Gotts et al., 2012). It has been proposed that deficit in perceiving the human movement might be related to abnormalities in the posterior superior temporal

sulcus (pSTS). Indeed evidence exists that it is structurally (Levitt et al., 2003; Boddaert et al., 2004; McAlonan et al., 2005; Barnea-Goraly et al., 2010; Noriuchi et al., 2010; von dem Hagen et al., 2011) and functionally (Di Martino et al., 2009; Philip et al., 2012) altered in ASD. Previous studies showed that activation in STS is modulated by the emotional content of the perceived stimuli, even at a supramodal level (Peelen, Atkinson, & Vuilleumier, 2010). Yet, our results showed that TMS over pSTS did not reverse the adaptation after-effect for emotional PLD, suggesting that the emotional significance of the observed human movement is not encoded by this brain region. This inconsistency may be due to the fact that STS activity is indirectly modulated by attentional and arousal mechanisms highly involved in emotion processing, likely mediated by the strong connection between STS and the amygdala (Amaral, Behnia, & Kelly, 2003; Iwai & Yuki, 1987; Iwai, Yuki, Wantanabe, Hikosaka, Suyama, & Ishikawa, 1990). Neuroimaging findings allow only correlative inferences about the implication of the activated brain area and previous studies demonstrated correlated but not necessarily causal activation of STS during the observation of bodily expressions. The integrity of superior temporal sulcus has been shown to be fundamental to biological motion perception (Grossman et al., 2000; Grossman et al., 2005; Saygin, 2007; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990), but critically the stimuli used in these studies displayed only neutral movements. Therefore, the role of pSTS in processing the emotional content of whole body expression remained unexplored. Our study fills this gap, suggesting that the posterior part of the superior temporal sulcus is not causally involved in the recognition of PLD's emotional content. A widespread network of brain areas underlies the comprehension of human movement and the integrated activity of aIPS and STS constitute a mechanism for the hierarchical representation of actions. In fact, it has been shown that aIPS and STS represent different aspects of human movement, with a low-level pictorial representation in pSTS and

a more abstract representation in the parieto-frontal system (Cattaneo et al., 2010). Likewise, it might be that the comprehension of emotional body expression requires a higher level of elaboration, which is computed in aIPS rather than in pSTS.

3.3.2. Interpretation of results in aIPS

The emotional body language is rich of information and its correct recognition requires a multilevel analysis. Indeed, when we observe an emotional whole body movement it is necessary to process the visual information about the shape of the body, to comprehend the action implemented and to identify the conveyed emotional significance. Therefore, it is not surprising that the perception of this kind of stimulus activates different brain areas, such as visual regions, regions associated with the limbic system, and areas associated with the encoding of motor information (Hadjikhani e de Gelder, 2003; de Gelder et al., 2004; Grèzes et al., 2007; van der Riet et al.,2009). The body movement is a nonverbal type of communication and - as the verbal - it involves production and comprehension abilities, which are acquired concurrently during development. When a bodily expression is perceived, the priority in our brain is to create a representation of the observed emotional movements to react promptly and adaptively (*Grèzes et al., 2007*). The putative MNS is a good candidate for being the common neural base for both processes as it is part of the action observation system and has connections with visual and limbic structures. In particular, the aIPS is strongly interconnected with motor, premotor and subcortical areas (Clower et al., 2001; Rizzolatti et al. 2014) and with STS (Arfeller et al., 2013; Nelissen et al., 2011) and therefore is a good candidate for being a key structure in emotional body perception (de Gelder et al., 2006). The intraparietal sulcus involves visuo-motor cross-modal integration (Grefkes et al., 2002) and is critical for determining grasp configuration based on perceptual features of the

object towards the action is directed. Furthermore, this region is selective not only for the current grasp action but also for the subsequent movement to be performed. The goal of the action is represented at a higher level in aIPS, and its function goes beyond preshaping the hand to match a target object (Tunik et al., 2007). Using the adaptation paradigm, neuroimaging studies in healthy subjects showed a sensitivity of aIPS to repetition suppression effects when an individual repeatedly observed similar objects and hand configurations (Shmuelof and Zohary, 2005) as well as action goals (Hamilton and Grafton, 2006; 2008). Also, motor experience-based reduction of activity has been identified within this region when participants observed graspable objects (Handy et al., 2006). Other studies showed that the majority of neurons in the IPS were differentially activated depending on whether the observed grasping was followed by bringing the object to the mouth or by placing it somewhere, suggesting that this area is responsible for chaining the action together (Fogassi et al., 2005). These motor chains represent the neural substrate for implementing the agent's motor intention. Neurons that encode a specific motor act within a given action are linked with neurons that encode the following motor act. Thus, motor chains that represent the entire action are formed: when an action-constrained hand grasping neuron becomes active, it triggers the whole motor chain in the observer, who in this way may understand the agent's intention. Therefore, the ability to chain together actions in a sequence allows to predict subsequent actions and infer intentions and could be a precursor to mentalizing and beliefs inference skills. In the last decade, it has been proposed that a deficit in in this motor chaining mechanism might account for the impairment in understanding others' behaviour in ASD (Cattaneo et al., 2007; Fabbri-Destro, Cattaneo, Boria, & Rizzolatti, 2009; Ferrari & Rizzolatti, 2014; Rizzolatti & Fabbri-Destro, 2010). In accordance with this theory, a study has revealed impaired ability to chain together the phases of a sequence of actions in children with ASD (Cattaneo et al., 2007) suggesting

that the difficulties in understanding others' intentions might indeed be related to a deficit in aIPS. Supporting this hypothesis, a single-cell recording study in monkeys revealed the existence of neurons in the parietal cortex which adapted their response to motor events according to the social context (Fujii, Hihara, & Iriki, 2007). Therefore, the integrated activity of STS, aIPS, and the premotor and motor cortices appear to constitute a mechanism for emotional comprehension and for preparation of action in response to perceived emotional signals. The body motion is visually encoded in STS and from there projected to aIPS. Here, visual and motor information are integrated and action chaining allows inference of the emotional meaning of the observed actions. At this point, aIPS communicates with PM and M1 to initiate a coherent behavioural response. Thus, aIPS has two functions: it enables the comprehension of the observed emotional movement and activates the related behavioural response. This implies that the impairment related to a malfunctioning of aIPS might lead to not only difficulties in understanding the observed emotional body movement, but also to deficits in executing the right behavioural response. In line with this assumption, Freitag et al. (2008) reported a correlation between imitation, dynamic balance and diadochokinesis ability and neural activation in aIPS during biological motion perception in the ASD group. In addition, a recent study found attenuated adaptation for biological motion in children and adolescents with ASD (van Boxtel, Dapretto, & Lu, 2016), which might be related to an altered functionality of the parietal cortices. Thus, it is possible that the impairment in ASD is not restricted to the understanding of observed emotional movement, but concerns also the activation of the appropriate behavioural response. Future research is needed to explore the relation between aIPS functioning in the ASD population during emotional body movement perception and its association with deficits in responding properly to those extremely social relevant stimuli.

3.4. Conclusion

For the first time we demonstrate the existence of an adaptation after-effect for emotional point-light displays. Our study demonstrates the existence of a mechanism in the human brain designated to the encoding of the emotional content of body movements, and locates it within the anterior part of the intraparietal sulcus. These findings may help to explain the difficulties that individuals with autism encounter in everyday social interactions and raise new perspective for future research in this direction.

Chapter 4

GENERAL DISCUSSION

Since its first breath, the human being is dip in a highly social environment that requires him/her to individuate other agents, to recognize their actions, intentions and dispositions, to perceive their emotional states, to represent other person's perceptions and beliefs and to share the attention with them. In one word, to interact. People with Autism Spectrum Disorder have important deficit in social interaction (American Psychiatric Association 2013). In the last decade, numerous findings have suggested that this impairment could be explained by difficulties in encoding the human body movements (Kaiser & Pelphrey, 2012; Kaiser & Shiffrar, 2009; Pavlova, 2012). In this field, contrasting evidence exists on the identification of neutral actions, while difficulties in emotion recognition have consistently been reported (see Pavlova, 2012 for a review). However, in most studies these abilities have been investigated with Point-light display (PLDs), while in the real life the people around us are fully-shaped. Therefore, the obtained results might just partially explain the problem, or even give biased explanations, as the used stimuli involve just an aspect of the body language (the motion) and are not realistic. Moreover, despite it is well known that individuals with ASD have uneven cognitive profiles, with non-verbal skills higher than verbal, most studies have adopted the full-scale IQ as matching criterion with control groups. Moreover, when emotion comprehension is investigated, often the task used has been the verbally report (Hubert et al. 2007; Parron et al. 2008; Moore et al. 1997). All those experimental choices could have masked the real difficulty in body motion recognition in ASD. Furthermore, it still remains unexplored whether the social difficulties are category-specific or generalized. In fact, a copious number of studies have investigated emotion recognition abilities in

single social domain (i.e. face, body, voice), but there are only few works comparing the emotion recognition across different classes of social stimuli in individuals with ASD (e.g. Philip et al., 2010). Another issue in the existing literature is that there is a big lack of studies involving people with LF ASD. Finally, just few research have adopted a developmental approach (Annaz et al. 2010). During my PhD I have tried to fill some of these gaps, exploring the ability in recognizing the emotional valence of human movements in people with ASD. In order to understand the contribution of body form and body motion information in emotional bodily expression comprehension, I have used Full-light (FLDs) and Point-light display (PLDs) of whole-body human movements. In order to understand developmental changes, I have compared this ability between children and adults. In order to understand the role of intelligence, I have included people with high- and low-functioning ASD, both in children and adults, using the non-verbal IQ as matching criterion and asking them to perform a non-verbal forced-choice task. In order to understand whether the impairment in comprehending social relevant signals in ASD was restricted to body movements or widespread to other social cues, I have used static and dynamic stimuli depicting facial and bodily expressions. Finally, in order to better understand the neural origin of this difficulty, I have investigated the brain substrate of body emotion recognition in a TMS study.

Here below I will briefly resume the results of all the studies explained in detail in Chapter 1, 2 and 3:

1. In the **first experiment**, we found that, in TD children, happiness was the hardest emotion to be disentangled when conveyed by body movements, while fear was identified fastest. Furthermore, the vision of body form, compared to the vision of pure motion information, facilitated the identification of the emotional body expression and partially made its elaboration faster. On the contrary, in children with ASD, we did not find any difference neither in Accuracy nor in RTs across emotional contents or lighting conditions (FLDs and PLDs).

When the performances of the groups were compared, TD children resulted more accurate but not faster than ASD; in turn HF ASD were more accurate but not faster than LF ASD. Our results confirmed previous findings showing an impairment in individuals with ASD in comprehending the meaning of body movements. However, our results suggested that, when the emotional content is correctly recognized, its processing requires the same amount of time in the three groups (equivalent RTs). Hence, it seems that, when the mechanism for body movement comprehension works in children with ASD – despite fewer times with respect to TD – its mode of operation is similar to that of TD children. Furthermore, our findings showed an impairment in recognizing fear as prior studies did. However, in our experiment the difficulty was not specific to fearful stimuli identification, but it was broadened to all the emotional contents. Finally, regression analysis showed that the accuracy was marginally predicted by age in TD children, while rapidity was predicted by IQ; in HF ASD both accuracy and RTs were predicted by both the age and IQ; in LF ASD accuracy was marginally predicted by IQ, and the interaction between IQ and age predicted the RTs. This means that, when the encoding of BM is intact (TD), the efficacy of this process improves with age (i.e. vaster experience and more mature brain structures) while its efficiency increases with higher cognitive levels (i.e. more efficient neural substrates). Whilst, when the processing of BM is impaired, both its efficiency and its efficacy are related to age and cognitive resources, suggesting that the experience and the cognitive resources contribute together in modulating the improvement in BM recognition. According to that, and since the neural systems coding for the body movement has been shown to be abnormal in ASD population, we hypothesised the existence of a compensatory mechanism which develops with age only in HF ASD. To test this hypothesis, we run the same experiment with adult participants.

2. In the **second experiment**, we found similar results to Experiment 1. In TD adults, happy body movements were recognized with least accuracy, and fearful movements faster than neutrals. With regards to the lighting condition, FLDs were recognized better and faster than PLDs. On the contrary, in adults with ASD no effect was significant. Contrarily to children (Experiment 1), we found that in the group of adults the accuracy did not differ between TD and adults with HF ASD, neither in FLDs nor in PLDs. But the TD were overall more rapid than HF ASD. Furthermore, adults with LF ASD performed less accurate and slower than both HF ASD and TD adults. Once more, we found an impairment that involved the comprehension of Fear, but it was not specific for threatening stimuli. In fact, the difficulty was also related to the identification of neutral and happy stimuli. These results are consistent with other studies adopting a forced-choice paradigm to investigate emotional body expression in ASD (Nackaerts et al. 2012; Atkinson 2009; Alaerts et al. 2014). Finally, analysis of regression revealed a relation between IQ and accuracy both in TD and HF ASD groups, while the IQ predicted the RTs only in TD adults. These results seems to confirm our initial hypothesis postulating a development of compensatory mechanisms only in the HF ASD group, that are mediated by high cognitive resources and improve with age. Although these mechanisms permit a better recognition of body movements, they have a cost in term of time processing. Possibly, they are not automatic and embodied as in TD (Vittorio Gallese & Cuccio, 2015), but are underlain by different systems.

3. In the **third experiment**, the comparison between children and adults has highlighted different evolutionary trajectories in BM recognition in the three groups. Within TD participants, adults were more accurate and faster than children; the vision of the body form facilitated the recognition of

body movements but it did not influence the rapidity of its processing (higher accuracy for FLDs compared to PLDs, but not different RTs). Moreover, happy body expressions were recognized with most difficulties, while fearful movements were recognized than the other emotional contents. The level of non-verbal intelligence and the age were significantly related to both accuracy and velocity, suggesting that the ability to recognize the significance conveyed by body movement continues to improve with age and that the amelioration of this capability is enhanced by high cognitive resources. Similarly to TD group, also within individuals with HF ASD the adults outperformed the children, but they were not more rapid. Conversely, and surprisingly, we found that children with LF ASD were more accurate than adults, while there was no group difference in RTs. Neither the emotional content nor the lighting condition modulated the performance in any of the ASD groups, suggesting a different processing of form and motion information and emotional content in these populations. Finally, in individuals with HF ASD but not in subjects with LF ASD, the accuracy improved in relation with IQ and age, and the RTs are marginally predicted by the IQ, confirming that the growing experience and the progressive maturation of neural substrate could modulate the improvement in comprehending the meaning of other people's movement only in presence of high cognitive resources.

4. In the **fourth experiment** we investigated whether the impairment in understanding social relevant signals in individuals with high-functioning autism was restricted to body movements or widespread to other social cues, such as facial expressions. Furthermore, we explored the role of implied or explicit movement in perceiving bodily expressions. To this aim, we asked participants to recognize the body expressions represented by dynamic or static stimuli. Finally, we presented both FLDs and

PLDs to investigate whether the vision of the body form, compared to the sight of pure motion information, could influence the identification of the emotional content of body movements. We did not find any group difference in accuracy in any of the class of stimuli. But there were group differences in RTs specific for the recognition of dynamic stimuli (TD were significantly faster than HF ASD in recognizing PLDs and marginally FLDs). These results suggest that HF ASD adopt compensatory mechanism to understand the meaning of facial and bodily expression that allow them to correctly recognize the emotional valence conveyed by face and body movements. This mechanisms are TD-likely efficient as far as the stimuli are static. However, when the information involve dynamic motion cues, the compensatory mechanisms become more sophisticated and have a cost in terms of rapidity. In fact, ASD needed more time to identify dynamic body stimuli, but not images of body expressions, suggesting a deficit in processing the actual body motion. What regards to the emotional significance, happiness was better recognized from facial expressions and was harder to be identified when expressed by body movements. Indeed, within body movements the comprehension of happiness results more difficult and time consuming than fearful and neutral actions.

Our behavioural data show an impairment in individuals with ASD in inferring the meaning of human body movements and possibly the adoption of compensatory mechanism along the development in people with high non-verbal abilities. But how can we explain these data at a neural level? Where do these difficulties origin? Where is the impairment located in the brain and which are the brain structures involved?

5. Our **TMS experiment** aimed to give an initial answer to these questions. Neuroimaging studies provided correlational data of functional and structural abnormalities in ASD brain during BM perception, involving in particular the posterior part of the superior temporal sulcus (pSTS) and the parieto-frontal nodes of the putative mirror neurons system (MNS) (Alaerts et al., 2014; Freitag et al., 2008; Herrington et al., 2007; Kaiser et al., 2010; Kaiser & Pelphrey, 2012; McKay et al., 2012; Nackaerts et al., 2012; Weisberg et al., 2014). However, to our best knowledge, the causal role of the pSTS and the anterior intraparietal sulcus (aIPS) in comprehending dynamic emotional human movements represented as PLDs has never been addressed in the same experiment before. Results from our TMS experiments are striking: we demonstrated that the aIPS, but not the pSTS, is crucial for encoding the emotional bodily expressions. Our results are consistent with a recent TMS study (Engelen et al. 2015) showing a causal role of the parietal lobe (IPL) in encoding fearful bodily expressions. Moreover, our data are in line with findings reporting abnormalities in ASD population related to this area (Cattaneo et al., 2007; Fabbri-Destro et al., 2009; Freitag et al., 2008; McKay et al., 2012; Rizzolatti et al., 2014; Rizzolatti & Fabbri-Destro, 2010) and reinforce the crucial importance of the role played by motor regions in empathising (Minio-paluello, Baron-cohen, Avenanti, Walsh, & Aglioti, 2008; Rizzolatti & Fabbri-Destro, 2010). In this experiment, we demonstrated that the aIPS is pivotal to infer the emotional content of human action. However, we do not pretend to explain the difficulties in interaction faced by individuals with ASD by addressing one single brain area as the only responsible for their social impairment, it would probably be over simplistic (A. Hamilton & Marsh, 2013). Hence, it is more likely that in ASD population the deficit in the aIPS is not isolated, but instead it is part of a wide dysfunctional network of brain areas, which, in a sort of out of tune chorus, contributes to define the social impairment.

Although in our experiment we did not register the brain activation in individuals with ASD, and thus it is not possible to directly correlate our behavioural data with the underlying neural substrates, I would try to insert our findings in a more broaden framework of aberrant neural organization referring to the existing literature. In the next paragraphs, I will review the neural and behavioural evidences of typical development of BM perception, differences between children and adults, and abnormalities in ASD population, in the attempt to give an all-encompassing explanation of our results.

Aged-related changes in bodily emotion recognition

First, our results showed that TD children aged between 5 and 11 years are able to correctly recognize the emotional valence of whole body movements, confirming previous research (Boone & Cunningham, 1998; Ross et al., 2012; van Meel et al., 1993). Furthermore, we found that, in TD individuals, adults were more accurate and more rapid than children in recognizing the valence of the whole-body movements, both in FLDs and PLDs. This result suggests that the development of processes involved in decoding bodily expressions continues from childhood to adulthood, in line with previous behavioural and neuroimaging findings (Boone & Cunningham, 1998; Carter & Pelphrey, 2006b; Peelen et al., 2009; Ross, de Gelder, Crabbe, & Grosbras, 2014; Ross et al., 2012; van Meel et al., 1993). Previous studies have showed an increasing specificity of cortical activity over age (Carter & Pelphrey, 2006b; Grill-Spector et al., 2006) and have led authors to suggest that different neural representation strategies are used across ages, possibly reflecting different spatial activity patterns within specialized cortical areas (Golarai, Liberman, Yoon, & Grill-Spector, 2010). Indeed, childhood and adolescence are periods of very dynamic brain modulation: in typical developing individuals the white matter myelination increases linearly about 12% between 4 and 22 years of age (Tomáš Paus et al., 1999), while contemporary the

grey matter decreases by 4 to 9% during this period (Sowell et al., 2003). The organization of brain morphology and neural circuits continues throughout childhood (Houston, Herting, & Sowell, 2014; Tomás Paus et al., 2005) and interconnected brain regions have been reported to exert mutual influence in developmental and maturation (Cao, Huang, Peng, Dong, & He, 2016; Stiles & Jernigan, 2010; Tau & Peterson, 2010). Accordingly, the brain regions involved in perception of social stimuli has been reported to undergo structural changes during the development (Gogtay et al., 2004), and functional MRI studies have shown different brain activity in children and adult while viewing other people moving with neutral or affective connotation (Ross et al. 2014; but see Peelen et al. 2009). In particular, the activation in the body selective areas (EBA, FBA, pSTS) was stronger and larger in adults than in children (Ross et al. 2014) during passive view of full-light videos depicting objects or emotional body movements. Altogether, our results and previous studies are in line in showing that the ability to recognize the significance of the body movements develops with age, together with the maturation of the underlying brain structures.

In the HF ASD group we found similar results to that of TD group, with adults outperforming children. However, since the brain structures underpinning the social cognition have been shown to be abnormal in ASD population (Gráinne M. McAlonan et al., 2005; Pelphrey, K. A., Shultz, S., Hudac, C. M. & Vander Wyk & Manuscript, 2012; Pelphrey & Morris, 2007), it is likely that ASD develop compensatory mechanisms with age, that improve their ability to comprehend the body movement. Our results corroborate this hypothesis, showing an impairment in children with HF ASD compared to TD controls, but a TD-like performance in HF ASD adults. The impairment that we found in children with ASD compared to TD controls might be due to a number of abnormalities reported in the ASD brain. Indeed,

research in ASD population showed aberrant morphology and pattern of connectivity since the very early stages of development. For instance, MRI and head circumference studies in ASD have shown an early brain overgrowth in the beginning of life, and subsequent slowing or arrest of growth during childhood and adolescence (Courchesne et al., 2007). This early overgrowth in ASD is not ubiquitous across the brain, but it mainly involves frontal and temporal regions, and it is explained with an excess in excitatory pyramidal neuron numbers. Interestingly, the overgrowth of white matter reaches its peak during the toddler years and the early childhood and this period coincides with the first moment in which children with ASD show differences from TD children in orienting to biological motion stimuli (Chawarska et al., 2014; Jones & Klin, 2013; Klin & Jones, 2008; Klin et al., 2002, 2009). Accordingly, atypical volume of grey and white matter and an overall enlarged brain volume have been reported in children with ASD as young as 1-2 years (Dawson et al., 2007; Dementieva et al., 2005; DISSANAYAKE, BUI, HUGGINS, & LOESCH, 2006; Hazlett et al., 2011) and 2-4 years (Carper, Moses, Tigue, & Courchesne, 2002; Courchesne et al., 2007; Hazlett et al., 2011; Sparks et al., 2002). During childhood the formation of circuits is exuberant, but the excess of excitatory neurons could profoundly disrupt it, producing a local over-connectivity and weakened and “noisy” long-distance functional interaction. This biases the spontaneous activity of local and long-distance networks preventing the automatic engaging with social-emotional cues. Critically, young children (2-4 years old) with ASD have short-distance connection dominating numerically and functionally the long-distance connection, and in 10-12 years old children with ASD the deficits in distribution of grey matter still encompasses brain regions with socio-emotional functions, such as the parietal and the temporal lobes (Gráinne M. McAlonan et al., 2005). Furthermore, an extensive white matter reduction in fronto-parietal, superior temporal and limbic areas, together with significant volume changes in reciprocal white matter connections, has been

reported also in adolescents with ASD (Barnea-Goraly et al., 2004) and in adults with Asperger's Syndrome (McAlonan et al., 2002). In the case of body movement processing, it has been proposed that this altered connectivity could diminish the flux of information from the temporal to parietal regions, making the social stimuli less salient and stunting the initial stages of human motion tuning and processing (McKay et al. 2012). The pSTS is important to provide a visual description of the observed body movement integrating form and motion information, but the comprehension of action goal and intention seems to occur in parietal and frontal areas of the so-called mirror neuron system (Rizzolatti et al. 2014) (see below "The role of motor system"). The pSTS is the main afferent of parietal regions, as a consequence the disruption of connection between temporal and parietal region from the early childhood up to adulthood might have an important implication for action understanding – emotional bodily expression included - in individuals with ASD.

Differences in body emotional valence recognition across different lighting conditions

Our results corroborate previous findings showing that the emotional valence of bodily expression is identifiable from the solely motion information (PLDs) (Atkinson et al., 2004, 2007; Dittrich et al., 1996; Ross et al., 2012). In addition, we found a difference in lighting conditions between individuals with ASD and TD, which informs us on the diverse elaboration of form and motion cues in these populations. Most of the previous research have investigated the BM perception in ASD using PLDs, and when difficulties were found, they were often ascribed to a Weak Central Coherence (Atkinson, 2009; Happé & Frith, 2006a). Interestingly, we found that the impairment in individuals with ASD was not specific for PLDs, but involved also the recognition of FLDs, suggesting that the difficulty in understanding the valence of the body expressions is related to a more general comprehension of human body

movements rather than to problems in integrating together the parts of an object. In fact, the WCC theory might explain difficulties in perceiving PLDs but not FLDs. Nevertheless, the results of our fourth experiment showed that participants with ASD were impaired in recognizing FLDs compare to TD controls, but that they reached a TD-like performance in recognizing the emotional content of full-light static body images, supporting the hypothesis of a specific deficit in processing the body motion information when dynamic.

Models of biological motion processing (Giese & Poggio, 2003; Lange & Lappe, 2006) suggest that the biological motion could be identified in two different ways: i) integrating form and motion information; ii) using only the form information. For what concerns the first strategy (Giese & Poggio 2003), it has been proposed the pSTS as the brain area where the information about the body motion and the body form are integrated (Beauchamp, Lee, Haxby, & Martin, 2003; Peuskens, Vanrie, Verfaillie, & Orban, 2005). The second strategy posits that actions are recognized on the basis of the concatenation of static *snapshots* of the observed body posture providing information about the direction of locomotion (Lange & Lappe 2006). At a neutral level, the right pSTS has been shown to be related to the processing of dynamic social information (Grossman et al., 2005), while the right EBA is primarily involved in the static analysis of body form (Atkinson et al., 2012; Downing et al., 2006). Using a cross-methodological approach (fMRI, TMS and behavioural), a recent study (Vangeneugden, Peelen, Tadin, & Battelli, 2014) has provided the causal evidence of a double dissociation between EBA and pSTS, confirming that form and motion information can be processed separately. In our experiments, we found that the vision of body form facilitates the recognition of biological motion valence in TD children and adults. On the contrary, within participants with ASD, we did not find any difference according to the lighting condition. Hence, it seems that in TD participants the vision of an additive characteristic (i.e. the body

form) improves the performance compared to the vision of the solely motion information. This means that the summation of form and motion cues is advantageous for TD individuals - as reflected by the more accurate and faster recognition of FLDs stimuli compared to PLDs - and suggests that the human body movement is encoded by integrating these characteristics. In fact, if form and motion information were processed separately, we should have found similar performance in the two lighting condition. Interestingly, this is exactly what we found in participants with ASD, suggesting that in this population the form and motion cues are not integrated but processed by independent mechanisms. Our results are consistent with neuroimaging studies, showing structural abnormalities in STS (Courchesne et al., 2007; Gráinne M. McAlonan et al., 2005; Zilbovicius et al., 2006) and functional STS aberrant activation during BM task in individuals with ASD (Kaiser et al. 2010; Freitag et al. 2008). Significant reduced connectivity between extrastriate visual regions and pSTS has also been reported using moving shapes simulating social interaction (Castelli, Frith, Happé, & Frith, 2002). Therefore, it is plausible that the impairment in pSTS and in its connections prevents the integration of form and motion information, limiting the ability to elaborate the body movements.

The posterior pSTS is also the main provider of visual input to the fronto-parietal regions of the action observation system (AOS) or “mirror network”, which is involved in action or emotion processing and in embodied cognition (Rizzolatti & Craighero, 2005) and has been previously implicated in ASD (‘broken mirror’ theory of autism) (Minio-paluello et al., 2008; Oberman & Ramachandran, 2007; Rizzolatti & Fabbri-Destro, 2010; Williams, 2008) (see below). In line with these research, the results of our TMS study (Chapter 3) demonstrate the importance of aIPS in encoding the emotional bodily expressions. On the contrary, although the pSTS has previously been shown to be responsible for perceiving neutral PLDs (Grossman et al. 2005), according to our results it does not seem to be critical for encoding the

emotional content of body movements. Interestingly, Freitag and colleagues (Freitag et al. 2008) reported hypo-activation of the inferior parietal lobule (IPL) and STS in ASD during a task of BM perception, and a negative correlation between severity of ASD and activation of IPS and STS. Accordingly, McKay et al. (McKay et al. 2012) showed a different neural activation and connectivity between adults with ASD and TD controls during BM perception. In particular, ASD group showed hypo-activation in the IPL and inferior temporal gyrus (ITG, an area overlapping with EBA), while responses in the fusiform gyrus (FFG) and in the occipital lobe were similar between groups. Furthermore, analysis of the connectivity showed a flux of information between ITG and the superior parietal lobule in TD participants, while in ASD group no activation of ITG/EBA was found but an atypical pattern of connectivity emerged between FFG and occipital areas. In line with that, Libero et al. (Libero et al., 2014) reported a weaker connectivity in adults and adolescents with ASD, between the visual areas and IPL during a task of human action identification. Therefore, it seems that in the autistic brain not only the brain areas that process the body movement are abnormal, but also their reciprocal connections appeared altered.

As discussed above, in TD individuals the form and motion information are integrated – likely in STS - but in the ASD brain this seems to be prevented by a disconnection between IPS and pSTS. However, according to the alternative model proposed by Lappe and Lange (Lange & Lappe 2006), the BM can also be recognized through a concatenation of snapshots. Interestingly, the Experiment 1 showed that TD children outperformed children with HF ASD both in FLDs and in PLDs, but in the Experiment 2 and marginally in the Experiment 4 we found that adults with HF ASD recognized the FLDs at a TD-like level. Therefore, it could be that in HF ASD an alternative mechanism for BM encoding based on the body form processing matures or is acquired with age. In the human brain, EBA (Downing et al., 2006) and

FBA (Peelen & Downing, 2005) contain neurons sensitive to body images. McKay et al. (McKay et al. 2012) reported an hypo-activation in ITG, an area overlapping with EBA, while responses in the fusiform gyrus (FFG) and in the occipital lobe were similar between groups of TD and ASD participants. Furthermore, atypical pattern of connectivity emerged between FFG and occipital areas, thus FFG could be a good candidate to process the static snapshot of human movements. Intriguingly, it has been shown a bilateral hypoactivation of FFG in ASD children, corroborating our results and hence the hypothesis that the mechanism based on the BM recognition through body form analysis develops with age.

The role of motor system in the emotion comprehension development

The disconnection between the parietal and the temporal areas have an implication for the understanding of the emotional bodily expressions. In fact, the parietal areas to which STS projects are part of the putative mirror neuron system (MNS). It has been proposed that MNS areas mediate the comprehension of observed others' actions through a "direct-matching mechanism" (Rizzolatti & Craighero, 2005). According to that mechanism, when an action is performed, in the agent's brain it is generated a motor schema which becomes active also when the same action is observed. This internal simulation of the observed action permits a direct matching between self and other, and this common activation underlies the understanding of the goal, feeling and intention of the observed person (Vittorio Gallese et al., 2004; Vittorio Gallese & Cuccio, 2015). As I have explained in Chapter 3, in the parietal node on the MNS, the sequences of an action are chained together, enabling the observer to infer the intentions beyond the perceived actions (Cattaneo et al., 2010; V Gallese, Fadiga, Fogassi, & Rizzolatti, 2002). Therefore, if there is a failure in integrating the information in pSTS, or if the

information generated in pSTS cannot reach the associative areas in parietal cortex, the internal mirroring of the observed action would be more difficult or less efficient (Alaerts et al., 2014; Cattaneo et al., 2007; McKay et al., 2012). Results of our TMS experiment showed that the aIPS is necessary for recognizing the emotional expression, demonstrating that this area is critical, not only for the comprehension of the neutral instrumental actions, but also for the emotional body movements.

Contemporaneously to the MNS discovery (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), also other researchers similarly argued for a connection between motoric production and perception (Bushnell & Boudreau, 1993; Lockman, 1990). Those authors have intuitively suggested that, when the child begins to produce a certain behavioural action, he/she will also have access to the meaning of perceptual cues associated with that action. Therefore, they sustained that motoric action is a necessary, if not sufficient, precondition for perceiving an emotion. In line with this position, it has been reported that specific emotional states are embedded in particular structural cues (J M Montepare & Zebrowitz-McArthur, 1988; Joann M. Montepare, Goldstein, & Clausen, 1987) and that TD adults use these motor cues to attribute emotions to the expressive body movements (de Meijer, 1989). Interestingly and accordingly, Boone and Cunningham (Boone & Cunningham, 1998) found a correlation between the developmental stage when the pattern of movements specific for body expression are developed in children (motor production) and the period in which the children begin to recognize the emotional body expressions (motor comprehension), corroborating the idea that the self serves as a proxy for the emotion processing (Lombardo & Baron-Cohen, 2011).

In individuals with ASD, a number of research have reported a dysfunction of the MNS (Cattaneo et al., 2007; Dapretto et al., 2006; Fabbri-Destro et al., 2009; Oberman et al., 2005; Williams et al., 2006). In addition, neuroimaging studies that have investigated the emotion perception in different domains in

individuals with ASD seem to converge in defining a broader deficit in processing the emotional stimuli, including faces (Harms et al., 2010), prosody (McCann & Peppé, 2003), words (R. Moseley, Carota, Hauk, Mohr, & Pulvermüller, 2012; R. L. Moseley et al., 2015), and body movements (Atkinson, 2009; Hubert et al., 2007; Nackaerts et al., 2012; Parron et al., 2008). Interestingly, all these studies have showed a common neural substrate being abnormally active during the elaboration of all the emotional stimuli: the motor system. Therefore, one possible explanation for the emotional impairment in ASD is that the integrity of the motor system is essential for comprehending the emotional meaning of surrounding stimuli.

It is worth considering that the motor system is the means of expression for emotions from the very beginning of life, the emotional movements are indeed the unique visible signals of the internal affective states, and especially before the development of language they are the only communicative channel. In children, the development of motor, social and language skills are tightly linked (Iverson et al., 2010; Lenneberg, Chomsky, & Marx, 1967) and it has been shown that the intrinsic significance of emotions is defined by the use of words: when the emotional action is named in the context of its expression, the link between the movements and the correspondent internal state is created (Moseley et al. 2012). In this way, the word is associated with the internal feeling and the motor correlates specific for the emotion, and the abstract significance of the emotion is incorporated within the neural substrates encoding for the emotional gesture (i.e. the motor system). In simple terms, action and emotion are linked. In children with ASD the motor disorders emerge early in development (Esposito, Venuti, Apicella, & Muratori, 2011; Esposito, Venuti, Maestro, & Muratori, 2009; Teitelbaum, Teitelbaum, Nye, Fryman, & Maurer, 1998). Accordingly, deficit in expressing the emotion have been reported in ASD (e.g. Macdonald et al., 1989b; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger,

2006). Therefore, it is plausible that the social and communicative difficulties in ASD arise from the motor dysfunctions, and likely the impairment in emotion recognition in ASD is linked to the deficit in expressing the emotions, which in turn depends on motor system alterations.

An out-of-tune chorus

As seen in the previous paragraphs, a number of neural abnormalities contribute in defining the complexity of the Autism Spectrum Disorder. Therefore, a deficit in a single area or a single aberrant pattern of connectivity cannot exhaustively account for the social impairment in people with ASD. In this paragraph I will try to ease the complexity of the autistic brain and behaviour drawing an analogy with an “out-of-tune chorus”. Several brain areas have been shown to be hypo- or hyper-active in individuals with ASD (e.g. superior temporal sulcus, fronto-parietal motor regions, fusiform gyrus, inferior temporal areas, amygdala, ventromedial prefrontal cortex, to cite only the areas related to the social stimuli encoding). This implies that the information processed in these areas is somehow altered. Imagine the brain areas as a group of out of tune singers: they are singing together, but each of them is singing badly. In a chorus, as in a neural network, a good individual performance is not sufficient for a good performance, but the synchronization is crucial as well. In fact, it is very important that the individuals pay reciprocal attention to the other chorus’ members in order to sing harmoniously. At a neural level, this reciprocal tuning is underlain by the white matter connections. In the autistic brain there is a mismatch between excitatory and inhibitory activation, mainly caused by an excess of pyramidal neurons, resulting in an overall noisy activation. Besides, there seems to be a lack in long-range connections together with a hyper short-range connectivity. This produces a fragmented encoding of information and deficits in communication between brain areas. For instance, the higher

visual areas are impaired in ASD, thus they send atypical signals to the motor system, through weakened and chaotic connections, and in turn the motor system (which is also impaired) processes the information in an abnormal manner. The output of this altered, noisy and disconnected processing is - not surprisingly – a disharmonic behaviour. Unfortunately, the social impairment is not the only deficit in ASD. In fact, this disorder is also characterized by language difficulties; stereotyped or repetitive behaviours; highly restricted and fixated interests; insistence on sameness; inflexible adherence to routines; hyper- or hypo-reactivity to sensory input or unusual interests in sensory aspects of the environment (American Psychiatric Association 2013). Metaphorically speaking, it is like the chorus - that already has its own problems - was singing in the same room where also other problematic choruses were singing all together. As the reader can imagine, it is a shambles. Likely, this is what happens in the autistic brain.

The question now is: why does the chorus sing so badly? Who is the responsible? One possibility is that the fault is of the choirmaster, who did the teaching wrong from the very beginning. In the case of Autism, it is possible that the choirmaster is the motor system. In fact, since the birth, the movement serves as a main communication medium. From the very first minute of life, the internal states, the emotions, the intentions, and the objectives are acted with movements (for example, when the newborns are hungry they cry and wave their body). But in individuals with ASD the motor system is impaired, therefore their movements are clumsy, clunky, and disharmonic. As I have explained above, the execution of an action generates an internal motor schema which is used to comprehend the same action executed by another person. When the internal schema matches with the observed movement, the action is comprehended. Since the individuals with ASD are awkward, the pattern of movements they use to perform an action are different from that of typical developing individuals, and so are the

generated internal schemas. As a consequence, when people with ASD observe an action performed by another person, in their brain there is not an internal schema that could be used for matching – and hence comprehending - the observed movement. Back to the analogy with the chorus, the choirmaster, who was supposed to mediate the acquisition of the singing skills, was not a very good singer.

Although pivotal and essential, the choirmaster is not the only responsible for the chorus' failures, the experience is also very important in modulating the neural substrates, and hence the behavioural outcomes. When a child implements a behaviour, the caregiver behaviourally reinforces or discourages the children's conduct, and verbally comments what is happening by naming the actions, the object towards the action is directed (e.g. "You are indicating the ball. Do you want the ball?"), the effects that the action produces and the related internal states (e.g. "You are happy now! You like playing with the ball!"). In this way the implicit significance (e.g. the happiness) is linked to a precise physiological state (e.g. the sense of wellbeing and euphoria associated with happiness), to an extrinsic action (e.g. waving the arms to the top, talking with a higher tone of voice, smiling), and to a context (e.g. play with the ball). At a neural level, the brain systems coding for those different aspects are linked together in an integrated and multimodal representation of the situation (Gallese, 2003; R. L. Moseley et al., 2015; Oberman & Ramachandran, 2007; Rizzolatti, Fogassi, & Gallese, 2001). In a similar situation, the behavioural responses of children with ASD can be – by definition - atypical. In fact, the excess of enthusiasm can produce emotional overload, which in turn produces behavioural deregulation. For instance, to express that they are enjoying a pleasant situation, instead of smiling they might start flapping their hands or fingers, jumping or running around, etc. Such impetuous and stereotyped behaviours are not typical signs of happiness and therefore they could be misunderstood by whom is observing the scene. As a consequence, the verbal labels used by the adult might not be coherent with

the child's internal state. Intuitively, this mismatch produces chaos. In the brain of typical developing children this mechanism allows the internal state to be mapped into the motor system through the generation of a shared representation. On the contrary, the erroneous interpretation made by the adult produces a mistaken representation of the intrinsic sensation in the motor system of the child with ASD.

But this is not the only problem. In the best case scenario, the adult correctly interprets the behaviour of the child with ASD and the verbal comments are coherent with the internal state, therefore the linking between limbic, motor and higher cognitive circuits occurs properly, hence, for example the flapping of the hands is associated with happiness. At this point, the motoric schema that the child with ASD allows for the happiness is different from that of a typical child (for sure, a TD child would not flap his hands, but he would probably smile instead). As a consequence, when the child with ASD observes a happy TD child, the direct matching between internal representation and observed movement is not possible, because the observed movement does not exist among the internal representations of the child with ASD, or even worse it does exist but it is associated with a different internal state. For all these reason, the comprehension of other people is an issue for people with ASD. However, not all is lost. Fortunately, the experience may also play a positive role by correcting what in principle went wrong. Indeed, individuals with ASD can learn to interpret the actions of other people, using alternative strategies, different from the internal simulation. In addition, to naming their child's actions, parents tend to verbally comment also the actions performed by other people in the proximal environment (e.g. "John is coming here. He is giving you the ball. He wants to play with you."). In doing so, the objectives, intentions, feelings, and emotions of the other people are linked to their motor behaviour. With the experience, the subject with ASD can learn that there are particular movements widely used

to express happiness, and that even though those movements are different from the one he/she uses to express joy, they refer to the same internal state. This implies that the comprehension of other people is no more mediated by the automatic and direct matching between the observed movements and the internal representations, but it is rather underlain by higher-order inferential cognitive processes. These compensatory mechanisms require an elevated level of intelligence to be learnt and adopted, and for this reason they can be managed only by individuals with high-functioning ASD. Accordingly, in our experiments we found that the ability to recognize the emotional valence of prototypical whole-body movements improves with age and reach TD-like performance only in participants with HF ASD, but not in participants with LF ASD.

The improving role of the experience in modulating the abnormal brain activation has crucial implications for treatments with individuals with ASD. For example, an improvement at the motor level could favour the creation of internal motor representations more similar to the movements performed by neurotypical individuals. This will enhance the comprehension of the observed agents, and in turn will increase the social skills of people with ASD. Furthermore, it has been suggested that the motor system have recurrent feedback connections with the high-order visual areas (Avenanti et al., in preparation; Rockland & Van Hoesen, 1994). Hence, an amelioration of the motor system – consequent to therapeutic interventions - could positively influence the activity in the interconnected high level visual regions (such as pSTS) through feedback modulations. Those high-order visual area are in turn connected with, and influence, the low level visual areas (Pascual-Leone & Walsh, 2001; Petro, Vizioli, & Muckli, 2014; Romei et al., 2016; Sillito, Cudeiro, & Jones, 2006), and both low and high visual processes have been shown to be abnormal in ASD) (for a review, see Simmons et al., 2009). Therefore, an improving of motor capabilities could have a cascade of positive effects on the neural systems that

underlie the processing of body movements (face included), increasing the ability to correctly encode their characteristics and successfully comprehend the social meaning that they convey.

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