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SOCIAL INTERACTION IN HUMANS: BIOLOGICAL AND PSYCHOLOGICAL BASES OF FACE PERCEPTION AND EMPATHY

Magali Batty, Emilie Meaux

► **To cite this version:**

Magali Batty, Emilie Meaux. SOCIAL INTERACTION IN HUMANS: BIOLOGICAL AND PSYCHOLOGICAL BASES OF FACE PERCEPTION AND EMPATHY. Social Interactions: Evolution, Psychology and Benefit, 2013. hal-03115555

HAL Id: hal-03115555

<https://hal.science/hal-03115555>

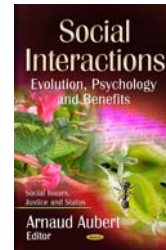
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Social Interactions: Evolution, Psychology and Benefits

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Editors: Arnaud Aubert (University of Tours, France)

Book Description:

Why are we social? Why most other animal species are? What are the pressures and benefits urging for social gatherings? And how are the necessary rules regulating social interactions built? Sociality and social interactions represent one of the most transversal topics in current research. The scientific approach of social interactions implies different theoretical and methodological perspectives, targeting the resolution of various complementary questions such as the causes of social behaviors, their dynamics, their development, their phylogenetic history, the attribution of social roles, and the modalities of synchronization and organization between individuals pursuing different or opposite goals, etc. This book gathers a set of contributions addressing the recent advances in the understanding of biological, neurological, psychological or socio-economic factors influencing social interactions in human and non-human (vertebrates and invertebrates) animals. (Imprint: Nova)

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Chapter

SOCIAL INTERACTION IN HUMANS: BIOLOGICAL AND PSYCHOLOGICAL BASES OF FACE PERCEPTION AND EMPATHY

Magali Batty and Emilie Meaux*

INSERM U930, Centre Universitaire de PédoPsychiatrie,
Tours, France

ABSTRACT

While the study of social behaviours has long been a main topic in ethology, the brain structures underpinning our social abilities have been investigated only recently. In the past twenty years, the number of studies focusing on how the brain processes the signals from others and how these signals influence our behaviour has increased impressively. A collection of brain regions involved in social cognition has been defined, referred to as the ‘Social Brain’. This chapter combines the biological and psychological approaches focusing on two domains of social neuroscience: face perception processing and empathy. While faces are arguably the most important visual stimuli we process every day, empathy constitutes a crucial psychological process that is the basis for much of our social interactions.

INTRODUCTION

As were our nonhuman relatives in evolution, humans are intrinsically and intensely social. From birth, we interact with people around us, and our survival relies on this dependency which continues long after the newborn’s attachment period. Our psychological and physiological well-being is critically dependent on our interaction with peers throughout life. We then possess a wide repertoire of social abilities, allowing us to detect quickly, automatically and efficiently the presence of another human being in our environment. Such

* E-mail: magali.batty@univ-tours.fr.

perception allows us to make inferences about emotions, beliefs and feelings. Moreover, we are able to use this knowledge to guide our interactions.

While the study of social behaviours has long been a main topic in ethology, the brain structures underpinning our social abilities have been investigated only recently. In the past twenty years, the number of studies focusing on how the brain processes the signals from others and how these signals influence our behaviour has increased impressively. A collection of brain regions involved in social cognition has been defined, referred to as the ‘Social Brain’ (Brothers, 1990). A vast neural network has been identified which extends from posterior areas, such as the superior temporal sulcus and the fusiform gyrus, more involved in social perception (voice, face, gaze, etc) to anterior regions such as the prefrontal cortex more implicated in higher level social processing (emotion regulation, mentalizing, etc), through sub-cortical structures such as the amygdala (for an overview, see Adolphs, 2003b).

Social interests appear early in human life. Only a few weeks after birth, newborns address more smiles to their caregivers and other people than to objects, suggesting that they discriminate social from nonsocial entities. At one year of age, infants are able to attract another’s attention by vocalizing or pointing. At around three years of age, the understanding of emotion progressively leads to the inference of mental states in others (theory of mind (Baron-Cohen, 1991; Baron-Cohen, Leslie, and Frith, 1985)). Children then start to take into account the feelings of others to adapt their behaviours. The acquisition of social abilities still continues until late adolescence (Blakemore, 2008; Blakemore and Choudhury, 2006; Steinberg and Monahan, 2007). The development and improvement of our social abilities is linked with the age-related changes in structural and functional neural correlates of social cognition, which are also dependent on appropriate experience of the environment.

Brain disorders can compromise the ability to perceive and respond to others. For example, autism is a neurodevelopmental disorder defined primarily by core impairments in social communication (APA, 2000) including unusual eye contact, limitations in expression of facial emotion and recognition, lack of understanding of other people’s thoughts and feelings, atypical social engagement and difficulty with peer relationships. Many of such clinical studies have reported both anatomical and functional abnormalities in the different areas of the wide brain network typically involved in social cognition in autism spectrum disorders. Similarly, in almost all social disorders, atypicalities have now been reported in the social brain (depression (Elliott, et al., 2012; Victor, Furey, Fromm, Ohman, and Drevets, 2010), schizophrenia (Derntl, et al., 2012; Volpe, Mucci, Quarantelli, Galderisi, and Maj, 2012), bipolar disorders (Keener, et al., 2012)).

This chapter combines the biological and psychological approaches focusing on two domains of social neuroscience: face perception processing and empathy. While faces are arguably the most important visual stimuli we process every day, empathy constitutes a crucial psychological process that is the basis for much of our social interactions.

1. FACE PROCESSING

Visual perception of a typical natural scene is extremely complex as it contains many objects, few of which may be relevant to an individual’s current behavioural goals. In order to

establish which objects are important, each one must be identified: our brain needs to evaluate the visual inputs and allocate more cognitive resources to particularly relevant stimuli and events. The human face is arguably one of the most important visual stimuli for human social interactions.

1.1. Fundamental Aspect of Face Processing in Social Cognition

The wealth of information contained in faces make them essential mediators of social communication. With a single glance at a face, even without language, we can obtain information about gender, age, identity, attractiveness, etc. Moreover, faces express emotions and allow detection of others' mental states. We process the information from faces everyday as it informs us how to behave socially: being able to discriminate whether the person coming towards you is your friend or your boss, and whether he looks angry or happy will certainly make a difference to how you interact with him.

1.1.1. Face and Attention

Because of their social significance, faces automatically capture attention when in competition with other non-face objects (Hershler, Golan, Bentin, and Hochstein, 2010; Hershler and Hochstein, 2005; Theeuwes and Van der Stigchel, 2006; Tomalski, Csibra, and Johnson, 2009; Wilson, Brock, and Palermo, 2010). In order to examine whether faces are able to attract our attention, several studies have used the visual search paradigm that requires the detection of an odd element, the target, in an array of distracters. The time to find the target is measured according to the number of distracting elements in the display. When the reaction time for the detection of the odd element is independent of the number of distracters, the odd element is said to "pop out" (Treisman and Gelade, 1980), reflecting a basic mechanism for the relevant feature. A number of earlier studies have shown that natural face stimuli do pop out among assorted animal faces or non-face objects (cars, clock, etc)(Hershler and Hochstein, 2005; Langton, Law, Burton, and Schweinberger, 2008; Nothdurft, 1993) whereas schematic and inverted faces (Tomalski, et al., 2009) do not pop out.

Kuehn and Jolicoeur reported that the pop out effect of faces is eradicated in a background of distracters containing facial features, and the search for a face becomes markedly easier when the distracters look less like faces (Kuehn and Jolicoeur, 1994). These results suggest that the capture of attention by faces could be linked to an overall perception of a stimulus such as a face.

There has been discussion in the literature regarding the causes of the advantage of face detection over other categories of visual stimuli (Cerf, Harel, Einhauser, and Koch, 2008; Hershler, et al., 2010; Hershler and Hochstein, 2005, 2006; VanRullen, 2006). For example, while Hershler and Hochstein (2005) argue that the face "pop out" is a high-level, 'holistic' effect, VanRullen (2006) considers that the pop-out effect is mostly based on low-level factors.

Visual attention to human faces has also been investigated through study of the ocular exploration of faces. Recording of ocular movements has revealed that faces are fixated very quickly (100ms) and preferentially compared to other stimuli (Crouzet, Kirchner, and Thorpe, 2010; Fletcher-Watson, Findlay, Leekam, and Benson, 2008; Yarbus, 1961), suggesting that visual attention is selectively oriented toward faces. This attraction of faces is not only

observed during a presentation in isolation but also during exploration of natural scenes. In a study in which two scenes were presented side by side, one containing a single person and the other not, investigation of gaze patterns during free viewing indicated a strong bias towards looking to the person-present scene. Faces attracted disproportionately many fixations, the preference emerging in the first fixation and becoming stronger in the following, confirming previous findings of ultra-rapid processing of complex information (Fletcher-Watson, et al., 2008).

Faces capture attention, and within the face some elements appear to attract the attention and the gaze of the observer particularly. In fact, eye and mouth regions hold the majority of our interest, probably because of their relevance for social communication. However, recent eye-tracking evidence clearly demonstrates that face exploration is not rooted in a single, or even preferred, information-gathering strategy (Miellet, Caldara, and Schyns, 2011). In some cases in this study, a given observer even identified the same face using local information on one trial and global information on another trial, depending on the location of the first fixation.

1.1.2. Eyes and Gaze

The eye region of a face represents a special area due to the extensive amount of information that can be extracted from it. More than other facial features, the eyes are central to all aspects of social communication: they are necessary for proper identity and emotion processing and indicate the direction of attention of others and their potential targets for intentions (Itier and Batty, 2009).

Like faces, eyes vary greatly from one individual to another and the eye region may thus be a key element of face recognition. In fact, face detection is disproportionately impaired when the eye region is occluded compared to when the nose, mouth, forehead (Lewis and Edmonds, 2003) or eyebrows (Sadr, Jarudi, and Sinha, 2003) are removed from the picture. Image classification techniques have also shown that the eye region is the diagnostic feature used to discriminate gender (Schyns, Bonnard, and Gosselin, 2002; Vinette, Gosselin, and Schyns, 2004) and to recognize identity (Caldara, et al., 2005). Moreover, when noise is added to the picture, identity discrimination between two faces is performed using the eye region including the eyebrows (Sekuler, Gaspar, Gold, and Bennett, 2004).

In addition to its important role in processing identity, the eye region carries information necessary for emotion recognition and is thus central to non-verbal communication. All six basic emotions described by Ekman (joy, fear, anger, sadness, surprise and disgust (Ekman and Friesen, 1971)) involve a specific change in the eye region. For example, fear and surprise are characterized by wide open eyes and by a larger white sclera size (Whalen, et al., 2004), the lower eyelid is contracted when the person is expressing fear but relaxed when expressing surprise. Anger is implied by frowning with the eyebrows and other eye cues (Smith, Cottrell, Gosselin, and Schyns, 2005), and sadness by a down-looking gaze (Ekman and Friesen, 1978). The eyes could be considered therefore as a 'window to the soul' and provide information regarding the emotions and the states of mind of others.

Another communicative function of eyes is to direct attention toward specific places and objects of the environment through gaze. If someone is looking directly at us then we are the object of their attention. Direct or mutual gaze is a prerequisite to social interactions. In contrast, when the gaze of someone is averted to a direction other than towards oneself, it informs us that we are not the object of interest and that the person is attending to something

or someone else (Baron-Cohen, 1995; Baron-Cohen, Jolliffe, Mortimore, and Robertson, 1997; Emery, 2000) and we then usually turn our attention towards this object.

In agreement with its social value, several studies have shown that the eye region is the facial feature to which most attention is paid and the most used source of information regardless of the task, whether it focuses on gaze, head orientation, identity, gender, facial expression or age (Henderson, Williams, and Falk, 2005; Itier and Batty, 2009; Itier, Villate, and Ryan, 2007; Schyns, et al., 2002). The eyes are the preferred attentional targets in the exploration of a face, and a normal adult devotes more attention and therefore time to this element during face perception. Moreover, in healthy adults, face exploration begins by looking at this socially relevant facial feature (Hernandez, et al., 2009). This attraction to the eyes is even more pronounced for familiar faces (Althoff and Cohen, 1999).

1.2. Cognitive and Neural Bases Involved in Face Processing

The social information conveyed by faces leads us to consider them as very special visual stimuli. Human adults are so remarkably proficient (expert) at recognizing faces, they can recognize thousands of individuals at a glance, even at a distance, in poor lighting, with a new hairdo, after 10 years of aging, or when the face is seen from a novel viewpoint. This ability is impressive and suggests the involvement of efficient and specific behavioural strategies and neural bases during face perception.

Several lines of evidence from cognitive psychology, neuropsychology, neurophysiology and more recently neuroimaging studies support this thesis of an autonomous processing system preferentially dedicated to faces. Moreover, descriptions of disorders such as prosopagnosia (selective impaired face recognition associated with normal or relatively good object recognition, (Bodamer, 1947)) also supply information supporting this thesis, indicating a dissociation between the mechanisms involved in perception of faces and objects (Duchaine and Nakayama, 2006).

1.2.1. Cognitive Mechanisms of Face-Specific Processing

Several behavioural studies have clearly found this dissociation between the processes involved in face perception and those involved in object perception. While objects are processed element by element (featural information), faces are processed as a '*whole*'.

All faces share specific features organized in the same specific configuration (i.e. the eyes are above the nose, the nose above the mouth). This common arrangement of facial features is called first order configuration. A second order configuration or second-order relational properties describe the fine-tuned metrics of the different facial features and thus are unique for each individual face. Finally, holistic information refers to the integration of featural and configural information into a single inseparable unit ('*gestalt*').

Although there is no consensus on which type of processing is in fact used during face perception (figure 1), some authors argue that faces are recognized using a more holistic representation than other types of stimuli (Farah, et al., 1998; Tanaka and Farah, 1993). On the other hand, many researchers consider that face perception relies more on 1st and 2nd order configural processing (Diamond and Carey, 1986). Bringing together these two theories in a single model, Maurer et al. proposed that face perception involves three distinct stages of processing. Initially, first-order relational information (two eyes above nose, nose above

mouth) is gathered, and this is then combined into a holistic gestalt-like representation. Finally, second-order relational information (i.e., spatial distances between facial features) is processed, allowing recognition of individual faces (Maurer, et al., 2002).

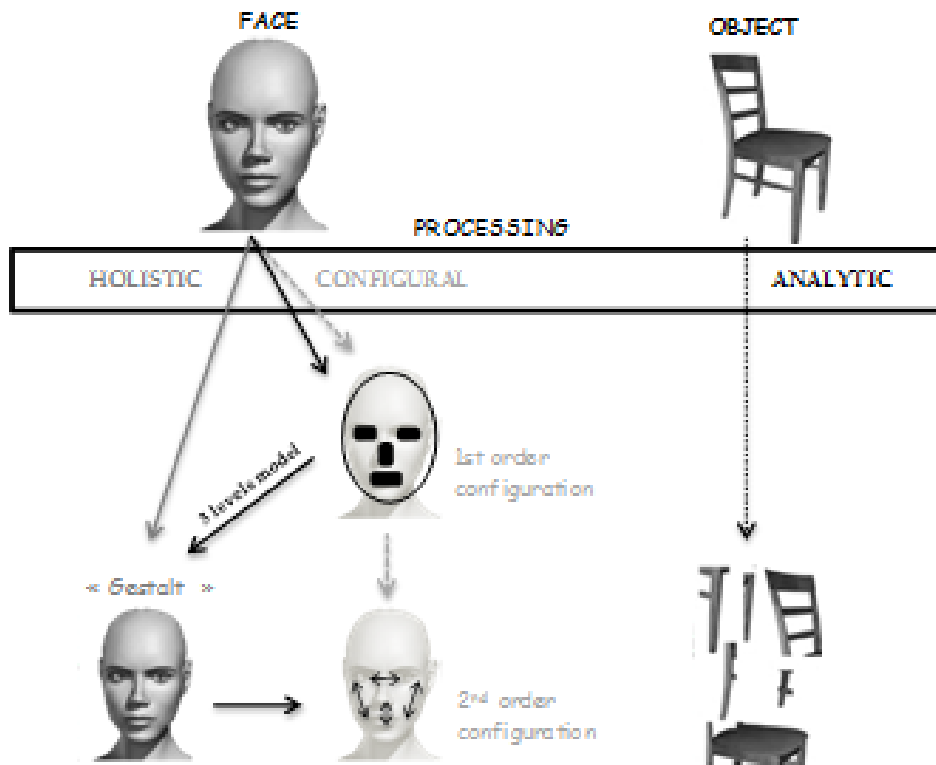


Figure 1. A specific processing of faces. Some authors suggest that face perception involves an overall representation of face (gestalt) (Farah, Wilson, Drain, and Tanaka, 1998) whereas others support the intervention of configural processing (Diamond and Carey, 1986). The black lines show the 3 level model proposed by Maurer et al. (Maurer, Grand, and Mondloch, 2002).

The best evidence for involvement of holistic and configural processing during face perception comes from different experimental manipulations of faces which specifically affect one of these processes.

The inversion effect (Freire, Lee, and Symons, 2000; Itier and Taylor, 2002, 2004c; Leder and Carbon, 2006; Rossion, Delvenne, et al., 1999), consisting of vertical inversion of the face, preserves the 2nd order configuration and the low-level visual features but disrupts the coding of 1st order configural cues. This manipulation impairs recognition of faces more than recognition of other classes of mono-oriented objects, suggesting a specific relationship between face recognition and first order configuration processing.

The Thatcher illusion¹ (Bartlett and Searcy, 1993; Boutsen and Humphreys, 2003; Thompson, 1980) disrupts the encoding of 2nd order configural information and leads to impairment of face recognition. Similarly, modulating the spacing of the different facial

¹ In the Thatcher illusion, the mouth and eyes are cut out, inverted, and pasted back into a face. When upright, the resulting face appears grotesque, but when inverted it appears normal, or nearly so.

features in natural limits (Maurer, et al., 2007; Mondloch, Le Grand, and Maurer, 2002) has confirmed that the 2nd order configural information is required to recognize facial identity.

Another important cue for both configural and holistic processing of faces is the part-whole effect or “whole advantage” (Tanaka and Farah, 1993). This term refers to the finding that participants are better at discriminating eyes or mouths when these parts are embedded in a full face than when they are shown in isolation. Another way to demonstrate the involvement of holistic/ configural processing in face perception is the composite effect: participants find it harder to identify one half of a composite face (e.g. top half of Barack Obama’s face with bottom half of Will Smith’s) if the inconsistent other half-face is spatially aligned with the target half rather than misaligned (Hole, 1994; Schiltz and Rossion, 2006; Young, Hellawell, and Hay, 1987).

However, one theory under debate suggests that configural processing is not unique to faces but is used with other categories of objects, particularly if, like faces, these objects are fairly homogeneous and the viewer has developed expertise in distinguishing individual aspects at the subordinate level (Carey, 1992; Diamond and Carey, 1986). This theory leads to the idea that the specific processes involved when perceiving faces might not be innate but might be the result of acquisition of face expertise.

1.2.2. Brain Correlates of Face Processing

Because most face processes are automatic, efficient and fast, it is easy to forget that face processing as a whole is indeed an extremely complex function, requiring encoding of shape (external and internal features) and surface properties (color, texture, brightness, etc) and also the analysis of subtle facial movements and social value (emotions, gender, mental states, etc). This complexity is confirmed by the extensive literature on the brain areas underpinning face processing which revealed that face perception is underlain by a large number of cortical and subcortical structures. However, within this extensive and distributed network, a core of particular face-selective regions has been identified in the right occipito-temporal cortex.

Functional magnetic resonance imaging (fMRI) studies have identified face-selective regions in the human cortex : the superior temporal sulcus (STS) (Haxby, Hoffman, and Gobbini, 2000; Haxby, et al., 1999; Kanwisher, McDermott, and Chun, 1997; Puce, Allison, Bentin, Gore, and McCarthy, 1998; Tanaka and Curran, 2001; Yovel and Kanwisher, 2005), the ‘occipital face area’ (OFA) (Dubois, et al., 1999; Gauthier, et al., 2000; Halgren, et al., 1999; Haxby, et al., 1999; Pitcher, Walsh, and Duchaine, 2011; Rossion, et al., 2000) and the ‘fusiform face area’ or FFA (Kanwisher, et al., 1997; Kanwisher, Stanley, and Harris, 1999; Sergent, Ohta, and MacDonald, 1992; Yovel and Kanwisher, 2004). Certain authors have suggested that these regions could be combined together to form the heart of a distributed cortical network specializing in face perception (Calder and Young, 2005; Haxby, et al., 2000; Ishai, 2008; Rossion, 2008).

The FFA region is known to be the site of the most consistent and robust face selective activation (Kanwisher and Yovel, 2006). Investigations of the specificity for faces of this cortical area per se began in the mid-1990s, and revealed that this structure responds more strongly to faces than to letter strings and textures (Puce, Allison, Asgari, Gore, and McCarthy, 1996), flowers (McCarthy, Luby, Gore, and Goldman-Rakic, 1997), and other stimuli, including mixed everyday objects, houses and hands (Kanwisher, et al., 1997). Moreover, the FFA is activated specifically in response to faces, and not to lower level stimulus features usually present in faces (such as a pair of horizontally arranged dark

regions) (Andrews, Schluppeck, Homfray, Matthews, and Blakemore, 2002; Kanwisher, Tong, and Nakayama, 1998; Rhodes, Byatt, Michie, and Puce, 2004). The FFA has also been shown to be involved in determining face identity: a higher FFA response was recorded in trials in which subjects correctly identified a famous face than when they failed to recognize the same individual (Grill-Spector, Knouf, and Kanwisher, 2004), implicating this region in face identity processing.

The OFA preferentially represents the physical structure (Kanwisher and Yovel, 2006; Liu, et al., 2003; Pitcher, et al., 2011; Rotshtein, Henson, Treves, Driver, and Dolan, 2005) and the parts (eyes, nose, and mouth) of a face (invariant aspects of faces)(Liu, Harris, and Kanwisher, 2010; Nichols, Betts, and Wilson, 2010; Pitcher, Walsh, Yovel, and Duchaine, 2007). These results suggest the involvement of the OFA in an early stage of visual perception. Indeed, a recent study proposed that the OFA is the first stage in a hierarchical face perception network in which the OFA represents facial components prior to subsequent processing of increasingly complex facial features in higher face-selective cortical regions (Pitcher, et al., 2011).

In contrast to the FFA and the OFA, the STS is not correlated with successful face detection (Andrews and Ewbank, 2004; Grill-Spector, et al., 2004; Kanwisher, et al., 1998). Andrews and Schluppeck (2004) presented ambiguous stimuli (Mooney faces) that were perceived as faces in some trials but as novel blobs in others. Whereas the FFA response was stronger for face than blob percepts (see also Kanwisher et al. 1998), the STS showed no difference between the two types of trial. These findings are consistent with those of Grill-Spector et al. (2004), who found that the response of the FFA was correlated with successful detection of faces in briefly masked stimuli, but the response of the STS was not. Instead of being involved in face detection and recognition, the STS region appears to extract other dimensions of faces such as their emotional expression, gaze direction and lip movement (variant aspects)(Haxby, et al., 2000; Hoffman and Haxby, 2000; Puce, et al., 1998).

While fMRI studies have provided information about spatial localization of brain activity associated with face processing, Event-Related Potentials (ERPs) recorded non-invasively on the scalp constitute a powerful tool for assessing the timing of cognitive functions ms by ms. In accordance with behavioral studies that reported fast ocular saccades toward faces (Crouzet, et al., 2010), many ERP studies have revealed that faces are processed at an extremely early stage, as early as 100-120ms after stimulus onset (Linkenkaer-Hansen, et al., 1998; Taylor, 2002; Taylor, Batty, and Itier, 2004), and some authors even suggest a faster process occurring before 100ms (Pourtois, Grandjean, Sander, and Vuilleumier, 2004; Pourtois, Thut, Grave de Peralta, Michel, and Vuilleumier, 2005).

Since the pioneering work of Jeffreys (1989) on the vertex positive potential (VPP) elicited by faces (Jeffreys, 1989), studies recording ERPs to pictures of faces have focused on a sequence of well characterized posterior components, most notably the P1 and the N170 components (figure 2). The visual P1 (or P100) is an early occipital component, peaking at around 100ms following stimulus onset, which is known to reflect an early stage of general visual processing. Approximately 70ms later (between 130 and 190ms post-stimulus onset), the P1 component is followed by a negative 'face-sensitive' electrophysiological response peaking at occipito-temporal sites, named N170 (Bentin, Allison, Puce, Perez, and McCarthy, 1996a).

Typically showing pronounced right-hemisphere lateralization, the N170 component is clearly and consistently larger in response to faces than non-face stimuli (“scrambled faces”, cars, pets faces, furniture, hands, houses, etc) (Bentin, Allison, Puce, Perez, and McCarthy, 1996b; Bentin, Degutis, D’Esposito, and Robertson, 2007; Halgren, Rajj, Marinkovic, Jousmaki, and Hari, 2000; Rossion and Jacques, 2008; Rousselet, Mace, and Fabre-Thorpe, 2004). Moreover, many studies have reported sensitivity of N170 to physical characteristics of faces such as size, orientation and inversion (Itier and Taylor, 2002; Jacques and Rossion, 2007; Rossion, et al., 2003; Rossion, Campanella, et al., 1999; Sagiv and Bentin, 2001) and also to isolated face parts, especially eyes (Bentin, Golland, Flevaris, Robertson, and Moscovitch, 2006; Itier and Batty, 2009).

Although delayed, N170 is even larger for eyes than faces (Bentin, et al., 1996b; Itier, Latinus, and Taylor, 2006; Jemel, George, Chaby, Fiori, and Renault, 1999; Taylor, Edmonds, McCarthy, and Allison, 2001). It was therefore initially suggested that it may reflect the processing of eyes rather than faces. However, when eyes are erased from the face, N170 is slightly delayed but of the same amplitude as for normal faces (Eimer, 1998; Itier, Alain, Sedore, and McIntosh, 2007), which suggests that this component reflects the configural (or holistic) aspect of face processing and not the activity of an eye detector (Eimer, 2000b; Rossion, Campanella, et al., 1999).

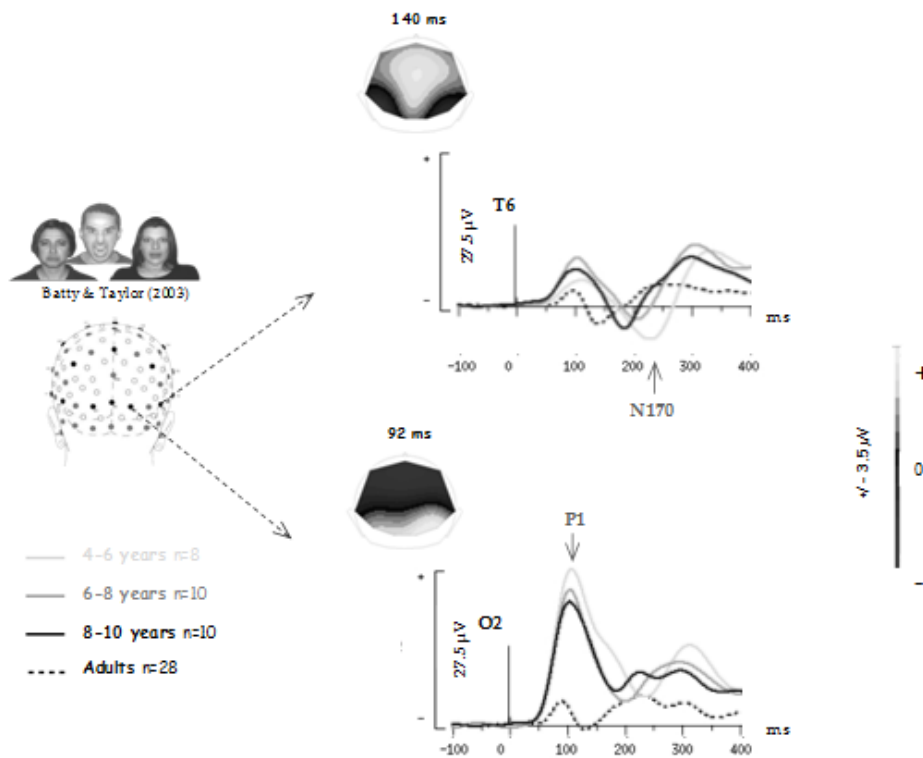


Figure 2. Development of ERPs recorded in response to emotional faces (used in Batty and Taylor, 2003) between 4 years of age and adulthood. P1 and N170 characteristics can be observed. The topography is presented in adults.

Moreover, the N170 component is also modulated by social information conveyed by faces. Gaze direction (Itier and Batty, 2009; Itier, Alain, et al., 2007; Taylor, et al., 2001; Watanabe, Miki, and Kakigi, 2002), repetition, familiarity (Caldara, et al., 2005; Holmes, Vuilleumier, and Eimer, 2003; Webb, et al., 2010) and facial expression of emotions (Ashley, Vuilleumier, and Swick, 2004; Batty and Taylor, 2003; Campanella, Quinet, Bruyer, Crommelinck, and Guerit, 2002; Eger, Jedynek, Iwaki, and Skrandies, 2003; Righi, et al., 2012; Smith, 2011) appear to affect N170. The N170 component therefore appears to be sensitive to the physical aspects of faces but it is also modulated by attention (Aranda, Madrid, Tudela, and Ruz, 2010; Eimer, 2000a; McPartland, Cheung, Perszyk, and Mayes, 2010). When attention is oriented toward faces using an explicit face perception task, the N170 component evoked by faces presents different characteristics compared to that registered in response to faces during an implicit perception task (i.e. faces are not attended to) (Taylor et al., 2004).

Source localization techniques have been used to identify the locations of the neural generators of this face component. Both the fusiform gyrus (Halgren, et al., 2000; Itier, Herdman, George, Cheyne, and Taylor, 2006; Itier, Latinus, et al., 2006; Rossion, et al., 2003; Rossion, Delvenne, et al., 1999) and the superior temporal sulcus (Itier, Alain, et al., 2007; Itier and Taylor, 2004d) have been identified as possible primary sources. Other source localization studies have reported the involvement of occipital extrastriate areas (Itier, Herdman, et al., 2006) or a relatively extensive network of sources located in both the temporal and occipital lobes (Corrigan, et al., 2009; Watanabe, Kakigi, and Puce, 2003).

Although P1 is not really specific to faces, some studies have reported face-sensitive effects on this earlier component (Eimer, 1998, 2000b; Halgren, et al., 2000). The P1 component is larger for faces than for other categories of stimuli (Taylor, 2002) and is affected by face inversion (Itier and Taylor, 2002; Linkenkaer-Hansen, et al., 1998; Taylor, et al., 2001) and expression of emotions (Eger, et al., 2003; Eimer and Holmes, 2002; Pizzagalli, REGARD, and Lehmann, 1999). However, these early effects are less consistent and appear to reflect low-level systematic differences between faces and other complex visual stimuli.

In summary, both fMRI and ERP studies have revealed specific brain activities in response to faces. Taken together, these lines of research make a compelling case for the existence of specialized cognitive and neural machinery for face perception per se (the face-specificity hypothesis).

1.3. Normal Development of Face Processing

Neonates orient preferentially towards faces. They preferentially track moving schematic faces, in contrast to other patterns of comparable complexity, including upside-down schematic faces (Goren, Sarty, and Wu, 1975; Johnson, Dziurawiec, Ellis, and Morton, 1991). Within days, babies have formed representations that support discrimination of their mothers' faces from a stranger's face. During the first 6 months, the baby comes to discriminate young from old faces, male from female faces. By 5-7 months, babies succeed in encoding new faces from minimal exposure, subsequently discriminating these from faces they have not seen before. Despite this astonishing level of proficiency in face recognition abilities already in the first days (Johnson, et al., 1991; Maurer, Holder, Espinola, Rupani, and Wilgis, 1983;

Pascalis, de Schonen, Morton, and Deruelle, 1995; Simion, Valenza, Umilta, and Dalla Barba, 1998; Valenza, Simion, Cassia, and Umilta, 1996), months (Fagan, 1972; Johnson, 1997; Maurer and Salapatek, 1976) and years (de Heering, Houthuys, and Rossion, 2007; McKone and Boyer, 2006; Sangrigoli and De Schonen, 2004; Tanaka, Kay, Grinnell, Stansfield, and Szechter, 1998) of life, behavioural studies have indicated that children's ability to recognize faces continues to show marked development until adolescence (Carey, 1992; Carey and Diamond, 1977, 1994; Chung and Thomson, 1995). In fact, the ability to recognize faces improves during childhood but an accuracy identical to adults' one can only be observed later (around 11 years of age (Feinman and Entwisle, 1976) or 16 years of age (Carey and Diamond, 1980) according to different studies).

To explain these findings, the theory of face expertise proposes that these age-related changes could be supported by the development of more efficient strategies to process faces throughout childhood. This hypothesis considers that the specific cognitive mechanisms involved in face processing (holistic and configural processing) may not be innate but may be acquired: from the maturation of an early interest in faces towards real expertise with faces throughout childhood. While young children use feature-based processing (analytic processing) to discriminate faces, a switch to a more holistic and configural processing of faces is reported at 10 years of age (Carey and Diamond, 1977) (figure 3).

The few studies investigating the anatomical and functional development of the brain correlates underlying this specific face processing are quite recent. Most of them have focused on age-related changes in the fusiform face area (Grill-Spector, Golarai, and Gabrieli, 2008), reporting an increase in the specialization of the FFA for faces from childhood to adulthood (Aylward, et al., 2005; Golarai, et al., 2007b; Passarotti, Smith, DeLano, and Huang, 2007; Scherf, Behrmann, Humphreys, and Luna, 2007). Children younger than 7–8 years of age do not show strong responses to faces in the FFA, and when activation in the FFA is detected in younger children, it is smaller than in adults or older children (Gathers, Bhatt, Corbly, Farley, and Joseph, 2004; Golarai, et al., 2007a; Passarotti, et al., 2003; Scherf, et al., 2007). Although, investigating the development of the other brain regions defined functionally as “face regions”, such as the occipital face area (OFA, (Rossion, et al., 2003)) or the lateral occipital complex (LOC, (Malach, et al., 1995)), studies have not reported an increase in specialization for faces with age, suggesting that these regions already show a preferential response to the relevant face category in childhood.

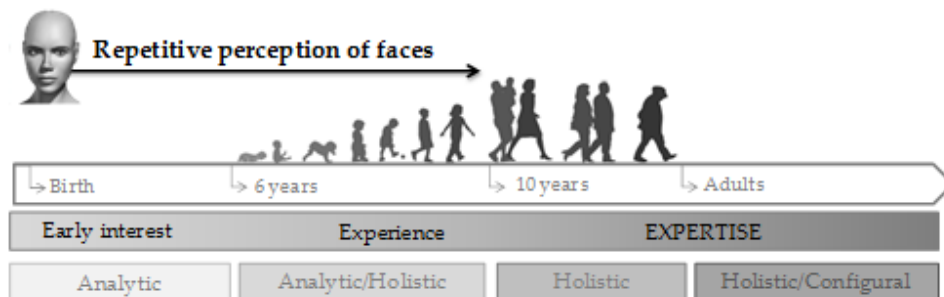


Figure 3. Maturation of face expertise. According to this hypothesis, configural and holistic processing are related to the development of face expertise (Diamond and Carey, 1986).

A recent study set out to characterize the entire set of brain regions or networks that are recruited for face processing in younger children (Joseph, Gathers, and Bhatt, 2011). The authors reported that some progressive changes (i.e. increases in face specialization with age) mostly occurred in the occipital-fusiform and inferior frontal cortex from 5 years of age until adulthood, whereas regressive changes (i.e. decreases in face specialization with age) emerged mainly in the parietal and lateral temporal cortices. Moreover, all of the regions involved in face viewing in adults were active in children, some regions already specializing in face processing by 5 years of age and other regions activated in children but not specifically for faces. Thus, it seems that neurodevelopment of face processing involves dynamic interactions between brain regions, including age-related increases and decreases in specialization and the involvement of different regions, at different ages (Joseph, et al., 2011).

In contrast to the fairly extensive adult literature on ERPs evoked by faces (N170, P1), only a handful of studies have examined their development between the ages of 5 and 16 (Kuefner, de Heering, Jacques, Palmero-Soler, and Rossion, 2010; Taylor, et al., 2004). The N170 component is a useful measure for the investigation of developmental changes in face processing, but additional and complementary information has also been acquired from the P1 component. In fact, P1 is very large and is easily measured in children, and offers an index of an earlier stage of visual processing than N170 (Taylor, et al., 2004).

The P1 and N170 components can be identified at the early stage of development (4-5 years of age)(Taylor, McCarthy, Saliba, and Degiovanni, 1999), suggesting that neuronal mechanisms underlying face processing similar to those seen in adults are present early in childhood. Nevertheless, the development of face processing with age appears to affect early neural responses (P1, N170) which reach the adult pattern only in the teenage years (figure 2). A meta-analysis of four prominent studies (Batty and Taylor, 2006; Itier and Taylor, 2004b, 2004c; Taylor, et al., 2001) which recorded ERPs to faces in children revealed large decreases in P1 amplitude with age, together with smaller, task-dependent, decreases in the latency of P1 throughout childhood (Taylor, et al., 2004). Important age-related changes in the amplitude, latency and scalp topography of the N170 component are also reported. Specifically, the latency of N170 decreases with age, as much as 100ms between 4-5 years and adulthood, the steepest decrease occurring before 10-11 years. The amplitude of N170, however, was reported to have a "U" inverted shaped developmental trajectory, the least negative amplitude being for children of 10-11 years. Children both older and younger than 10-11 years are reported to have larger (more negative) N170 amplitudes. Moreover, the topography of the N170 component in children is marked by dominant posterior positivity rather than negativity, with adult-like topographical activity emerging in the mid-teenage years (Taylor et al., 2004). It has also been reported that N170 was often bifid in young children (in two thirds of young children), having both an early (N170a) and later (N170b) peak. In older children and adults, only a single N170 peak was observed. This bifid peak in young children could be the result of two different anatomical generators in the lateral temporal or occipito-temporal cortices. These separate sources could fuse with age and brain development, or be due to slight architectural shifts only one being seen by surface electrodes.

Age-related changes in ERPs evoked by faces from 4 years until adulthood are commonly associated with developmental changes in face processes. In particular, the developmental changes in P1 have been attributed to an increased ability to perceive faces holistically. Similarly, it has been reported that maturation of N170 is related to an increased reliance on holistic and configural processing strategies (Taylor, et al., 2004). With age, face

processing becoming faster and more efficient with development, as face-sensitive cerebral activation is modulated. However, a recent study by Kuefner and colleague has reconsidered this theory (Kuefner, et al., 2010). The authors proposed that improvement in face processing tasks and cerebral modulation of its neural basis with age is not specific to the development of an effective ability to perceive faces per se but may rather be a product of age-related improvements in general sensory or cognitive functions, or general visual pattern recognition (visual acuity, sustained attention, etc) (Crookes and McKone, 2009; Want, Pascalis, Coleman, and Blades, 2003).

The development of typical face processing during childhood involves maturation of both perceptual and social information processing (Bhatt, Bertin, Hayden, and Reed, 2005; Carver, et al., 2003). These two explanations are thus not exclusive. The maturation of face processing is certainly sustained by the combined development of general sensory perception and acquisition of face expertise (holistic/configural processes).

1.4. Atypical Face Processing in Autism Spectrum Disorder (ASD)

Impairments in processing faces may represent a core deficiency in several brain disorders and may be central to abnormal social cognition. For example, people with the diagnosis of autism spectrum disorder, major depression or schizophrenia all have in common some difficulties in extracting the relevant information from these fundamental social cues and present abnormal cerebral activation in response to faces.

Autism spectrum disorder (ASD) is a neurodevelopmental disorder characterized by impairments in social interaction, communication, and restricted or repetitive interests and behaviours. Atypical face recognition is widely argued to be important for or even at the core of the social impairments of people with ASD (Dawson, Webb, and McPartland, 2005; Schultz, 2005). Therefore, over the past several decades many studies have investigated face processing in ASD to improve understanding of the social dysfunctions that are the hallmark of the disorder. Many studies involving children and adults have reported that individuals with ASD show selective difficulties with face recognition and discrimination (Boucher and Lewis, 1992; Boucher, Lewis, and Collis, 1998; McPartland, Dawson, Webb, Panagiotides, and Carver, 2004; Tantam, Monaghan, Nicholson, and Stirling, 1989), and also in extracting emotional cues from them (Boraston, Blakemore, Chilvers, and Skuse, 2007; Clark, Winkielman, and McIntosh, 2008; Kamio, Wolf, and Fein, 2006; Riby and Hancock, 2008; Weeks and Hobson, 1987; Wright, et al., 2008). However the number of studies finding the same or mixed performance of people with ASD in comparison to typical individuals for seven prominent markers of typical face processing (face inversion effect, part-whole effect, composite effect, inner vs. outer features, face space, Thatcher illusion and left side bias) (Weigelt, Koldewyn, and Kanwisher, 2012) suggest that some compensatory mechanisms might be involved in face recognition in autism (Bolte, et al., 2006; Grossman, Klin, Carter, and Volkmar, 2000; Spezio, Adolphs, Hurley, and Piven, 2007).

Some researchers have argued that it is the holistic or configural aspect of face perception that might be compromised in ASD (Dawson, et al., 2005; Faja, Webb, Merkle, Aylward, and Dawson, 2009; Gauthier, Klaiman, and Schultz, 2009; Teunisse and de Gelder, 2003). Their proposals are in accordance with more general perceptive theories (the Weak Central Coherence (Frith, 1989) or Enhanced Perceptual Functioning (Mottron and Burack, 2001))

postulating that individuals with autism use a cognitive style characterized by piecemeal or local processing, rather than context driven or global processing.

Clinical reports and behavioural studies have also shown that individuals with autism avoid eye contact (Hobson and Lee, 1998) and consequently show abnormal gaze patterns when exploring faces (Hernandez, et al., 2009; Snow, et al., 2011). Eye tracking studies have demonstrated that typically developing (TD) subjects made more fixations to faces than to nonsocial objects, whereas individuals with autism (ASD) did not differ in the number of fixations made to each stimulus type (Snow, et al., 2011). Moreover, although both the TD and ASD groups showed a strong preference for fixating the eyes more than the mouth, subjects with autism spent less time on the eye region than TD subjects (Hernandez, et al., 2009).

A recent paper reviewed 18 fMRI studies investigating face activation in ASD published between 1999 and mid-2009 (Perlman, Hudac, Pegors, Minshew, and Pelphrey, 2011). From the 15 that reported investigations involving the Fusiform Gyri (FG), ten reported hypoactivation in participants with autism compared to neurotypical participants (Critchley, et al., 2000; Dalton, et al., 2005; Hubl, et al., 2003; Humphreys, Hasson, Avidan, Minshew, and Behrmann, 2008; Koshino, et al., 2008; Pelphrey, Morris, McCarthy, and Labar, 2007; Pierce, Muller, Ambrose, Allen, and Courchesne, 2001; Piggot, et al., 2004; Schultz, et al., 2000; Wang, Dapretto, Hariri, Sigman, and Bookheimer, 2004), while five reported equivalent FG activity in participants with and without autism (Bookheimer, Wang, Scott, Sigman, and Dapretto, 2008; Hadjikhani, et al., 2004; Kleinhans, et al., 2009; Pierce, Haist, Sedaghat, and Courchesne, 2004; Pierce and Redcay, 2008). As illustrated by Perlman and colleagues, the state of the literature on the face processing system in ASD is currently quite undecided. However, it has been suggested that the abnormal FG activation can be accounted for by known differences in the visual scanpaths exhibited by individuals with autism in response to faces (Perlman, et al., 2011). One clever study reported “normalization” of activity in the right FG when individuals with autism were compelled to perform visual scanpaths that involved fixing upon the eyes of a fearful face. These findings have important implications for our understanding of social brain dysfunction in autism, the role of the FG in face processing, and the design of more effective interventions for autism (Perlman et al., 2011).

Investigating face ERPs in ASD, McPartland and colleagues found that the previously described N170 component was delayed in adults with autism compared with controls, with no inversion effect, suggesting not only a slower processing of faces but also a qualitatively different processing strategy (McPartland, et al., 2004). This latency delay was also reported in other studies using faces (Grice, et al., 2001; O'Connor, Hamm, and Kirk, 2005) or isolated eyes and mouths (O'Connor, Hamm, and Kirk, 2007). Other studies reported abnormal modulation of the potentials evoked by spatial frequency filtered faces (de Jong, van Engeland, and Kemner, 2008) and by emotional faces in ASD (Akechi, et al., 2010). However, one study reported normal ERP components in children with autism during both implicit and explicit processing of emotional faces (P1 and N170), although source analyses revealed abnormalities in the strength and dipole orientation of these components (Wong, Fung, Chua, and McAlonan, 2008).

These behavioural and neural deficits in face processing in ASD could be the result of decreased social motivation (Dawson, et al., 2002; Dawson, et al., 2005) that corrupts the development of face processing skills. However, there is increasing evidence that the cause of

the abnormal face processing in ASD could not be social in nature but may be related to perceptual abnormalities (Barthélémy, Hameury, and Lelord, 1995; Batty, Meaux, Wittemeyer, Roge, and Taylor, 2011; Behrmann, Thomas, and Humphreys, 2006; Bruneau, Roux, Adrien, and Barthelemy, 1999; Hyde, Zatorre, and Peretz, 2010; Lelord, 1990). For example, in one recent study (Batty, et al., 2011), analysis of the early ERP responses to faces (P1 and N170) suggested that the emotional and facial processing difficulties in autism could start from atypicalities in visual perceptual processes involving rapid feedback to primary visual areas. Also in accordance with this hypothesis, Hyde et al. (2010) reported abnormal grey matter increases in primary visual brain areas in autism and interpreted this result as the structural brain correlate of atypical visual perception in autism.

Thus, faces are arguably one of the most relevant visual stimuli used in social interactions in everyday life, and many studies have revealed the involvement of specific cognitive mechanisms and brain correlates during face perception that support slow age-related changes during normal development. In developmental disorders such as ASD, impairments in processing faces represent a core pathological disorder that leads to abnormal social cognition.

Using facial information and other social indices, empathy is another domain of social neuroscience that constitutes a crucial psychological process at the basis of many of our social interaction. Indeed, understanding other people's thoughts and feelings is essential to establish social engagement and peer relationships.

2. EMPATHY

The success of social interaction depends not only on the ability to detect cognitive and emotional processes in others, but also to the ability to interact with each other in effective and appropriate ways. For example, when one is misunderstood by a friend and feelings are hurt, one cannot feel rancour toward the friend if one knows he did not intend to hurt. However, strong resentment would be felt if he voluntarily scorns or belittles. Empathy results in a better understanding of another's actions, intentions and feelings and then possibly promotes prosocial and helping behaviours.

2.1. Theory of Mind, Empathy: Entangled Concepts

Two distinct but nevertheless linked cognitive mechanisms have been described: the theory of mind and empathy. The attribution of mental states, such as desires, intentions and beliefs, to other people by abstract inference has been referred to as theory of mind (ToM) or mentalizing (Fritt and Frith, 1999; Premack and Woodruff, 1978). Empathy has been described as the ability to infer and share another's experiences (Gallese, 2003).

However, a broad definition of the term empathy has also been proposed by Hoffman (2000) as: any process where the attended perception of the object's state generates a state in the subject that is more applicable to the object's state or situation than to the subject's own prior state or situation (Hoffman, 2000). In 2002, Preston and de Wall defined empathy as not

focusing on the response evoked in a subject but on the processes, the cognitive mechanisms involved. According to their model (Perception-Action Model), empathy is a superordinate category that includes all subclasses of phenomena that share the same mechanism, including emotional contagion, sympathy, cognitive empathy, helping behavior.... These phenomena all share aspects of their underlying process and cannot be totally disentangled (Preston and de Waal, 2002). According to some authors, the ability to understand and share another person's perspective, i.e. empathy, appears to involve theory of mind (Baron-Cohen, 2009; Shamay-Tsoory, 2011). Theory of mind is being able to put yourself in somebody else's shoes, being able to imagine what is going on in his or her mind (Baron-Cohen, 2009). It has been suggested that ToM represents the cognitive system of empathy (Baron-Cohen and Wheelwright, 2004). However, in his neuroanatomical model of empathy, Shamay-Tsoory (2011) considered that ToM is not a monolithic process and that it involves cognitive as well as affective aspects of mentalizing. So, imagining someone else's thoughts or feelings (ToM) is only part of empathy. The other part is having an appropriate reaction.

Thus, empathy is also a broad concept that can be divided in two separate systems (Kalbe, et al., 2007; Shamay-Tsoory, 2011; Shamay-Tsoory, Tomer, Goldsher, Berger, and Aharon-Peretz, 2004): an emotional system and a cognitive system. *The capacity to experience affective reactions to the observed experiences of others or share a 'fellow feeling' has been described as emotional empathy. On the other hand, the term cognitive empathy describes empathy as a cognitive role-taking ability, or the capacity to engage in the cognitive process of adopting another's psychological point of view* (Shamay-Tsoory, 2011). In other words, affective empathy includes sharing of another person's feeling while cognitive empathy involves cognitive understanding of another's point of view.

Being able to understand our conspecifics' mental and affective states constitutes a central aspect of social cognition affecting the quality of our relationships. This ability is a highly specialized, human-specific skill that forms a crucial prerequisite to functioning in social groups (Adolphs, 2003a; Herrmann, Call, Hernandez-Lloreda, Hare, and Tomasello, 2007) and is thought to be an important precursor to and motivator of prosocial behavior (Zahn-Waxler, Radke-Yarrow, Wagner and Chapman, 1992; Eisenberg, 2000). Empathy can lead to helping behaviour, but it can also lead to manipulation and hurtful behaviour (de Wied, van Boxtel, Zaalberg, Goudena, and Matthys, 2006). Conversely, the deficiency in empathy skills in psychopathic populations is believed to contribute to morally inappropriate behaviour (Blair, 2007; Soderstrom, 2003).

As empathy is an essential part of normal social functioning, several tools have been proposed to achieve its measurement. The assessment of Theory of Mind has been predominantly confined to so-called 'false belief' tasks. Such tasks intend to test the comprehension of another person's wrong belief (i.e. Smarties test (Hogrefe, Wimmer, and Perner, 1986), Sally-Ann (Baron-Cohen, et al., 1985)). During false belief tasks, children are typically presented with a scenario with two characters, during which one of the characters places an item in a given location and leaves the room. Then, the second character arrives and moves the item to a new location. When the first character re-enters the room, the participating child is asked where the first character will look for the item. If the child has a theory of mind, he should respond with the original location rather than the true location, thereby indicating a capability to see the situation from the (limited) perspective of the character who left the room (Wellman, Cross, and Watson, 2001). The Theory-of-Mind test (TOM test) designed by Steerneman (Steerneman, 1994) is a developmental tool. The TOM

test contains a variety of items that can be allocated to three subscales which correspond to the three main developmental stages of theory of mind (Flavell, Miller, and Miller, 1993): emotion recognition, understanding of false beliefs, and second-order beliefs. As a practical tool, the test provides information about the extent to which a child possesses social understanding, insight and sensitivity, and the extent to which he or she takes the feelings and thoughts of others into account. The empathy quotient (EQ (Baron-Cohen and Wheelwright, 2004)) is a short self-rated questionnaire designed for adults of normal intelligence. The EQ reveals a sex difference in empathy (female superiority) and an empathy deficit in Asperger syndrome and high functioning autism.

2.2. Cognitive and Neural Bases Involved in Empathy

Empathy is a complex neuropsychological function mediated by a complex neural network including the medial prefrontal cortex (mPFC), the superior temporal sulcus region, the temporal pole (Frith and Frith, 2003) and the amygdalae (Adolphs, 2003b).

According to some authors, empathy requires two systems: the perspective taking system and the mirror neuron system (Decety and Lamm, 2006b). While these two systems interact to create empathy, the mirror neuron system, also referred to as simulation theory or motor/emotional contagion, is automatic and shared by other species, *perspective taking is a more advanced system and involve higher cognitive functions* (Shamay-Tsoory, 2011).

2.2.1. The Mirror Neuron System (MNS): From Motor Resonance to Emotional Contagion

Over the last twenty years, several experimental studies involving humans and monkeys have suggested that observing another's action activates a similar representation in the brain to the one activated when executing this same action. This motor resonance when observing and executing an action leads to shared representation between the observer and the actor and has been referred as simulation theory.

In 1992, di Pellegrino and colleagues (di Pellegrino, Fadiga, Fogassi, Gallese, and Rizzolatti, 1992) revealed a set of neurons in the macaque (located in F5 area) that fire both when an action is performed and when a similar action is observed passively. These neurons, called mirror neurons, were later observed in the inferior parietal cortex (Gallese, PierFrancesco, Kohler, and Fogassi, 2002). An analogous mechanism has also been evidenced in humans in the inferior frontal gyrus, the inferior parietal lobule and the STS (Rizzolatti, 2005). However, it has recently been suggested that the mirror activity is widespread in the human brain. A recent meta-analysis of 125 studies confirmed the involvement of a core network of brain areas in visualizing and executing an action, including the inferior frontal gyrus, dorsal and ventral premotor cortex, and the inferior and superior parietal lobule (Molenberghs, Cunnington, and Mattingley, 2012). This study also revealed additional areas with mirror properties more involved in somatosensory, auditory and emotional processing (Carr, Iacoboni, Dubeau, Mazziotta, and Lenzi, 2003; Gazzola, Aziz-Zadeh, and Keysers, 2006; Lamm and Decety, 2008).

These mirror neurons respond not only when observing or executing certain actions, but also respond to the interaction between the subject of the action and the object and/or the goal

of this action. Activation of the MNS is thus involved in understanding the intentions of others, suggesting it could have a crucial role in the prediction and anticipation of an observed action (Iacoboni, et al., 2005). Such a mechanism of motor resonance could thus be helpful in social cognition, and could be extended to emotional processing. The tendency to automatically synchronize affective expressions with those of another person (mimicry) could sustain the understanding of emotional states of others and then allow access to their intention and motivation.

2.2.2. Neural Bases Involved In Empathy

Many lesion studies (e.g., (Eslinger, et al., 2007; Happe, Brownell, and Winner, 1999; Siegal, Carrington, and Radel, 1996; Winner, Brownell, Happe, Blum, and Pincus, 1998) and functional imaging studies (e.g., (Brunet, Sarfati, Hardy-Bayle, and Decety, 2000; Gallagher, et al., 2000; Vogeley, et al., 2001)) suggest that empathy, ToM and other social cognitive functions are mediated predominantly by a network lateralized in the right hemisphere, although evidence for bilateral (e.g., (Hynes, Baird, and Grafton, 2006; Vollm, et al., 2006)) and left-sided involvement also exists (e.g., (Baron-Cohen, et al., 1999; Calarge, Andreasen, and O'Leary, 2003; Fletcher, et al., 1995; Goel, Grafman, Sadato, and Hallett, 1995)), probably depending on task type and modality (Kobayashi, Glover, and Temple, 2007).

According to a recent review (Carrington and Bailey, 2009), the findings of the many imaging studies that have attempted to identify the neurobiological basis of ToM are heterogeneous (probably due to the heterogeneity of the paradigms used: recognition of mental state terms, single frame cartoons, comic strip cartoons, interactive games, etc). However, the authors revealed a pattern of regions involved: the medial prefrontal and orbitofrontal region was implicated in nearly all studies (93%), the anterior temporal lobe – including the amygdala – was activated in 38% of the studies, the superior temporal regions in 50%, the anterior and paracingulate cortices in 55%, and the temporo- parietal junction in 58% (Carrington and Bailey, 2009).

The medial prefrontal cortex and the orbito-frontal region: Gallagher and colleagues (2000) presented participants with both stories (auditive modality) and cartoons (visual modality) requiring the comprehension of the characters' mental state or not. They revealed that both ToM cartoons and stories elicited activity in the medial prefrontal cortex (Gallagher et al., 2000). Kobayashi et al., 2007 conducted an investigation of modality-related ToM (visual (cartoons) vs auditive (stories)) quite similar to that of Gallagher et al. (2000), however the task was more cognitively demanding and involved second order false beliefs. The findings revealed a more dorsal activity in the PFC that has been interpreted to be the result of the additional inhibitory control demanded by the attribution of second order false beliefs. This dissociation of ToM function within the mPFC has also been evidenced by two studies by Mitchell and colleagues (Mitchell, Banaji, and Macrae, 2005; Mitchell, Macrae, and Banaji, 2006). In the first study (Mitchell, et al., 2005), participants had to judge how the face presented was similar to their own face. The findings demonstrated a negative correlation between the extent to which participants judged the face to be similar to their own and the activity in the dorsal mPFC, and a positive correlation in the ventral mPFC. In the second study, the subjects were asked to pair a face with a description of political, religious and social views, which were either similar or dissimilar to those of the participant. Here again, they found greater activity in the VmPFC when the pairing was based on similar views, while the DmPFC was more active during judgments about dissimilar views. As previously

mentioned, empathy requires the distinction between actions generated by the self from those of others. Recent studies have revealed that the VmPFC and the temporo-parietal junction are largely responsible for these shared representations of self and others (Mitchell, 2009; Zaki and Ochsner, 2009).

Similarly, Eslinger suggested that different regions in the prefrontal cortex may be relevant for distinct functions, with a dorsolateral prefrontal cortex (DLPFC) system mediating cognitive empathy and the orbitofrontal cortex mediating affective empathy (Eslinger, 1998). Shamay-Tsoory et al. confirmed the special role of the ventromedial prefrontal cortex (VmPFC) in processing affective ToM (Shamay-Tsoory, Tomer, Berger, Goldsher, and Aharon-Peretz, 2005) and argued that cognitive ToM may involve both the VmPFC and dorsal parts of the prefrontal cortex (Shamay-Tsoory and Aharon-Peretz, 2007). Moreover, evidence from neuroimaging in lesional and psychiatric disorders has shown dissociation between the cognitive/emotional neural networks (Kalbe, et al., 2010).

Based on simulation theory, several studies on empathy have investigated the neural networks activated when observing pain in others and when we are in pain ourselves (de Vignemont and Singer, 2006; Decety and Lamm, 2006a; Jabbi, Swart, and Keysers, 2007; Wicker, et al., 2003). The *anterior cingulate cortex and the insula* were reported to respond to both felt and observed pain (Decety, Echols, and Correll, 2010). For example, Singer and colleagues (2004) measured the pain-related brain activation when pain was applied to the scanned subject or to his/her partner (Singer, et al., 2004). The results revealed that the anterior insula and the anterior cingulate cortex were activated during both the first-hand experience of pain and the observation of the beloved partner experiencing pain. These overlapping regions represent a crucial part of the human interoceptive cortex and subserve neural representations of internal bodily states such as information about temperature, hunger and bodily arousal states. Their activation may correspond to the generation of both a feeling and an affective motivation, with its concomitant autonomic effects helping us to understand the emotional significance of a particular stimulus and its likely consequences (Singer and Lamm, 2009). Finally, the anterior insular cortex is also involved in processing sensations and emotions such as taste or disgust (Jabbi, et al., 2007; Wicker, et al., 2003) in both first hand and vicarious experiences.

Other studies have revealed that the *temporo-parietal junction (TPJ)* has a central role in ToM, being involved in the attribution of agency to others, the self/others distinction and the representation of false beliefs (Kobayashi, et al., 2007; Lamm, Nusbaum, Meltzoff, and Decety, 2007; Sommer, et al., 2007).

In order to investigate the brain areas involved in the attribution of intention to other people, Völlm and colleagues (2006) used comic strips depicting a short story, and then asked participants to make a choice between two pictures that represented two possible story endings. Different conditions involving different kinds of stories and different instructions were used. Participants had to make their choice answering either 'what will the main character do next?' or 'what will make the main character feel better'. While the first did not involve social or emotional situations the second required the subject to empathize in an emotional way with the characters. The results confirmed an overlapping but distinct neural network for these two conditions. The emotional condition was associated with enhanced activation of the paracingulate, cingulate and *amygdalae* (Vollm et al., 2006). In another study, amygdala activation was found when subjects were asked to infer mental states from isolated eyes (Baron-Cohen, et al., 1999). The authors argued that such activation does not

simply reflect emotion-processing as the stimuli used *involve judging expressions of broad range mental states, many of which are not primarily emotional (e.g. interest, reflective, ignoring)*. Finally, amygdalar damage has been associated with impaired ToM processing (Shaw, et al., 2004). However, this study revealed that early damage to the amygdala leads greater impairment of ToM reasoning than late acquired amygdalar damage, suggesting the amygdala may have an important role in the neural systems supporting the normal development of ToM.

The recent large number of imaging studies has greatly advanced our understanding of which brain areas are responsible for making judgments about other people's behaviours, such as their goals, intentions, desires and beliefs. The obvious conclusion is that there is not a centre for empathy, but a strong neural widely extended and interconnected network that allows us to understand and manoeuvre in our social world. In a review covering more than 200 fMRI studies, Van Overwalle and Baetens confirmed that the mirror and mentalizing system studies identified two different systems, each specializing in the processing of observed sensory or verbal information about others but based on different types of input (Van Overwalle and Baetens, 2009). The meta-analysis revealed that these two systems are never concurrently active. This result might have led the authors to conclude that these two systems are disconnected, and that neither system aids or subserves the other. However, they claimed that researchers often design tasks to be as pure as possible in order to reveal specifically one of the systems, leading to a lack of understanding of how the two types of information interact in real-world situation. However, it appears to be a transition from the activation of the MNS to an activation of the brain areas involved in ToM and empathy (Shamay-Tsoory, 2011; Van Overwalle and Baetens, 2009).

The temporal dynamics of neural activities underlying empathic processes remain poorly investigated and hence understood. While ERPs offer precise information about temporal brain activation, only a few studies have used this technique to date to investigate the time course of empathy.

Following the idea that empathy may rely on basic resonant mechanisms that allow mapping of others' sensations onto one's own sensorimotor system, Bufalari and colleagues recorded somatosensory-evoked potentials while participants were exposed to video clips showing pain and tactile stimuli delivered to others (Bufalari, Aprile, Avenanti, Di Russo, and Aglioti, 2007). P45 is a positive component peaking over central-parietal electrodes at about 45ms after the stimulus, and is known to reflect the activity of the primary sensory cortex. P45 amplitude was found to be affected by observation of pain and touch in others. These results indicate that the primary sensory cortex is not only involved in the actual perception of pain and touch but also has an important role in processing the pain and touch of others by extracting somatic features from social interactions.

Fan and Han recorded ERPs in healthy adults who were presented pictures of hands that were in painful or neutral situations (Fan and Han, 2008). Their results provided electrophysiological evidence for the existence of both an automatic process and a controlled process of empathy for pain. An early differentiation between painful and neutral situations was recorded over the frontal lobe at 140ms after the presentation of the image. This early effect was correlated with the subjective report of the degree of perceived pain in others and of self-felt unpleasantness. Moreover, this early frontal effect was automatic as it was not affected by the task demand. The authors suggest that this early response reflects the encoding of the emotional content of the stimuli and possibly early emotional sharing. Later,

the P3 component recorded over the central-parietal regions also revealed a differentiation between the painful and neutral situations, which was affected by top-down attention to the pain cues (eliminated when the subjects were engaged in a counting task that drew their attention away from the pain cues). This late controlled process was interpreted as reflecting evaluation and appraisal of stimuli showing others in pain. Proverbio and colleagues recently investigated the time course of brain activation when observing two other people interacting (Proverbio, et al., 2011). Interestingly, they wished to distinguish two types of interaction, a cooperative interaction (e.g., 2 people dragging a box) or an affective interaction (e.g., 2 people smiling and holding hands). These two perceptually similar social interactions were discriminated on the basis of the agents' intention (cooperative vs affective goal) as they activated different brain regions. The inverse solution revealed the strongest sources in the right posterior cingulate cortex for affective actions and in the right STS for cooperative actions. The findings also indicated that the mirror neuron system (MNS) is more strongly activated by cooperative than affective actions, in agreement with the MNS being involved in the visuo-motor transformation of actions and action representation (indicated here by the parietal N2). The premotor and prefrontal areas are later involved in more complex social processing (P300).

To conclude, both fMRI and ERP studies have confirmed psychological evidence and have distinguished two different empathizing systems: an affective and a cognitive component (Decety and Jackson, 2004). Similarly, these studies with different approaches agree that empathy is based not only on a bottom-up process (automatic and unconscious) but also on a top-down process (controlled), these two processes being fundamentally intertwined. According to Decety and Lamm (2006), the bottom up process, perceptually driven and automatic, accounts for representation sharing (action, intention, feeling...), while through executive functions the top-down process generates an empathic response and modulates lower levels, adding flexibility and then making the subject less dependent on external cues (Decety and Lamm, 2006a; see also Singer and Lamm, 2009).

2.3. Normal Development of Empathy

Social preferences can be observed in very young children. As stated above, newborns preferentially orient their gaze towards faces rather than to other objects. After few weeks, they address more smiles to their caregivers than to others or to objects, indicating an early social preference. At around one year of age, they are able to orient another's attention with pointing and/or vocalizing. Children then progressively develop social strategies such as lies or jokes. At 5 years of age, they are able to use lie strategies to protect someone (Reddy, 2008). Similarly, although they perceive the emotions expressed by faces early, they will not comfort someone expressing sadness before 4-5 years old. At this age, children can also feel proud, or embarrassed, confirming their ability to take into account another's feelings in their own emotional feelings. While these pro-social behaviours induced by the ability to empathize are only observable after 4-5 years of age, early signs of empathy, beginnings or prerequisites might be present more precociously.

Indeed, as early as 18 to 72 hours following birth, newborns exposed to the sound of another infant crying display distress reactions, a phenomenon referred to as reflexive crying (Martin and Clark, 1982). Moreover, this personal distress seems to be specific to others'

negative emotional experiences, as infants do not show reflexive crying when exposed to their own previously recorded crying (Simner, 1971). This early emotional contagion supports the idea that there is a biological predisposition for interest in and responsiveness to the negative emotions of others. Meltzoff and colleagues demonstrated that newborn infants (only few hours old) can imitate adults' facial gestures (mouth opening and tongue protrusion) (Meltzoff and Moore, 1983). Facial imitation of emotional expression has also been revealed in human newborns (Izard, 1982) and at 10 weeks of age (Haviland and Lewica, 1987). This ability of newborns to imitate provides evidence that the observation and execution of human acts are innately combined and might be based on the mirror neuron system. This early arousal in response to others' signals *can serve as an instrument for social learning, reinforcing social exchange* (Decety, 2010).

While the reflexive crying and the early ability to imitate are thought to be precursors to empathic concern, young infants still have only basic capabilities for emotion, the development of self-other differentiation and perspective-taking is crucial for empathy.

Rochat (2003) proposed 5 levels for the development of self-awareness (Rochat, 2003). Immediately after birth infants are already capable of demonstrating a sense of their own bodies as a differentiated entity, they differentiate between self- and non self- touch, between stimuli oriented to their own body or external cues. Then at the end of the second month, infants start to have a sense of how their own body is situated in relation to other entities in their environment, in agreement with the findings on facial imitation (Meltzoff and Moore, 1983). At this age, infants explore the perceptual events they produce themselves in the environment (e.g. turn taking). It is only by 18 months that the next level is reached: children refer explicitly to their own body while exploring their mirror image, an identified self is clearly expressed, *the birth of 'Me'*. At approximately three years of age, children begin to grasp the temporal dimension of the self, children are capable of identifying themselves not only in the immediacy of the mirror experience but also in pictures and movies taken in the past. Finally at around 4-5 years of age, the last level allows children to be aware of how they are in the minds of others, *the public outlook on the self*.

This meta-awareness of the self, acquired by 4-5 years of age, is a crucial step to access to false belief tasks and ToM. In order to believe that another person holds a false belief, the child necessarily understands that he himself holds the right belief. Similarly, while the basic emotions seem to develop early in life, the development of the comprehension of more complex social emotions, also referred to as secondary emotions, such as pride, guilt and embarrassment is slower (Lewis, 2000). The understanding of these secondary emotions requires that the child is able to imagine what others might perceive or judge about himself, the level of *the public outlook of the self*. However, emotion recognition continues to develop until late adolescence (Tonks, Williams, Frampton, Yates, and Slater, 2007).

Cognitive components have a more protracted course of development than affective components, even though many precursors are already in place early in life (Decety, 2010). For example, joint attention, basically defined as the capacity to coordinate one's own visual attention with that of another person that depends on the ability to perceive direction of eye gaze (Baron-Cohen, 1995; Wicker, Michel, Henaff, and Decety, 1998), is a complex social executive function that emerges in the first year of life (Mundy and Jarrold, 2010).

Empathy does not only involve the ability to share others' points of view/ feelings and intentions, but empathy is based on the ability to develop a response to others' inputs that needs to be socially appropriate and sufficiently flexible. To this end, empathy rests on an

important cognitive component: the regulation of emotion. This component develops throughout childhood and adolescence, and parallels the maturation of executive functions (Decety, 2010; Zelazo, 2004).

The progressive development of empathy can be also observed in the development of goal-directed social behaviours, pro-social behaviours such as altruistic helping. Zahn-Waxler and colleagues have conducted extensive longitudinal studies examining the typical development of such empathy-related behaviours. In response to the simulated distress of a stranger or of their parent, between the ages of 14 and 24 months children manifested significant development in empathic concern (e.g., sad look) and pro-social behaviours (e.g., hugs), (Knafo, Zahn-Waxler, Van Hulle, Robinson, and Rhee, 2008; Zahn-Waxler et al., 1992). In fact, nearly all toddlers engaged in some helping behaviour in response to real and simulated distress by two years of age. Furthermore, the quality of pro-social behavior developed over the second year of life. The youngest infants' responses comprised primarily physical actions, whereas by 18 to 20 months toddlers were capable of a wide variety of helping behaviours, such as verbal comfort and advice, sharing, and distracting the person in distress (Zahn-Waxler et al., 1992). By the third year of life, young children were capable of a variety of empathy-related behaviors, including expressing verbal and facial concern and interest in another's distress, and they continued to engage in a variety of helping behaviours.

Years of brain maturation are necessary for the full expression of empathy. A large number of MRI studies investigating the neural development throughout life indicates that most social brain areas undergo protracted development until late adolescence (for a review, see Blakemore, 2008; Burnett, Sebastian, Cohen Kadosh, and Blakemore, 2011).

Developmental anatomical studies have revealed that the thickness of the grey matter in some frontal, temporal and parietal areas evolves according to an inverted U shape, with a maximum reached at adolescence (Giedd, et al., 1999). This local increase until adolescence, due to the augmentation of the number of synaptic connections, is then followed by progressive pruning leading to a thinning of the grey matter. This subsequent pruning, probably occurring via experience-dependent mechanisms, then results in more finely tuned and efficient neural circuits responding in an optimal way to the underlying complex and social functions. In parallel, the volume of the white matter increases regularly throughout adolescence (myelination), improving the speed of neural signals (Paus, et al., 1999). This increase is particularly marked in high level associative brain areas involved in complex cognitive functions.

Beside this structural developmental change, the functioning of these social brain areas also shows substantial developmental changes. An fMRI study investigating the neural bases of ToM through false belief tasks in children (8-12 years) and adults (Kobayashi, et al., 2007) found greater ToM condition-related brain activation in the superior temporal gyrus and in the vmPFC in the children's group than in the adult group. In contrast, the only region which showed significantly greater activity in the adult group than in the children's group was the amygdala, indicating that adults were more aware of emotional cues than children. Also comparing the cortical false belief network in children (10-12 years) and adults, while congruent data were reported for the PFC (i.e. greater activation in children than in adults), the temporo-parietal junction appeared not to be selectively activated in children (Sommer, et al., 2010). These results suggest that adults may utilize different brain regions in understanding ToM from children, far beyond the time children successfully master false belief tasks.

The greater activation of the mPFC in adolescents than in adults has been extensively reported (Blakemore, den Ouden, Choudhury, and Frith, 2007; Burnett, Bird, Moll, Frith, and Blakemore, 2009; Wang, Lee, Sigman, and Dapretto, 2006). For example, Wang and colleagues (2006) found that children (9-14 years) engaged frontal regions (mPFC) more than adults when engaged in an irony comprehension task. In the same vein, Blakemore et al. (2007) reported that when answering questions about the intentional causality of a previously seen scenario, adolescents (12-18 years) activated the mPFC more intensively than adults. However, they also reported that adults activated the STS more intensively than did adolescents. Although the same neural network is active, the relative roles of the different areas change. The neural strategy for thinking about intentions changes between adolescence and adulthood, reflecting the qualitative shift in the nature of social thinking such as adolescents are more self-aware and self-reflective.

Only a few ERPs studies have investigated false belief reasoning in adults, and they have reported a frontal late slow wave (LSW) (Sabbagh and Taylor, 2000; Liu, Sabbagh, Gehring, and Wellman, 2004), presumably reflecting the activity of the PFC. In young children (4-6 years of age), this LSW ERP component has been identified in children who understood false belief, but not in children who failed to show false belief reasoning (Liu, Sabbagh, Gehring, and Wellman, 2009). These ERP findings are in agreement with the fundamental role of the PFC and of the age of 4-5 years being crucial in accessing the ability to attribute mental state and to empathize with others.

Developmental studies thus provide unique opportunities to see how the components of empathy interact, helping us to understand the neural processes. They can also assist interventions in individuals with atypical development such as autism spectrum disorders.

2.4. Disorders

Autism is diagnosed when an individual shows abnormalities in social and communication development in the presence of marked repetitive behaviours and limited imagination (APA, 2000). It has been proposed that autistic children are socially impaired precisely because they lack a Theory of Mind (Frith, 1989).

This impairment of mind reading has been extensively demonstrated, children with autism failing at false belief tasks (Baron-Cohen, Leslie, and Frith, 1985) and scoring poorly in the ToM-Test (Muris, et al., 1999). Similarly, adults with high functioning ASD or Asperger syndrome scored significantly lower on the Empathizing Quotient (EQ) than typically developed adults (Baron-Cohen and Wheelwright, 2004), confirming a serious impairment of empathy abilities in ASD. Moreover, the above study revealed that the EQ is inversely related to the Autism Spectrum Quotient (AQ, Baron-Cohen, Wheelwright, Skinner, Martin, and Clubley, 2001). As noted above, empathy is a complex construct that requires many other functions. The literature reports difficulties in almost all of these functions (i.e. self concept, emotional processing, imitation, eye gaze processing, joint attention and regulation in ASD (Adrien, et al., 1995; Lombardo, Barnes, Wheelwright, and Baron-Cohen, 2007; Mundy, Sigman, and Kasari, 1990; Pelphrey et al., 2007; Rogers and Penington, 1991; Senju and Johnson, 2009; Senju, Kikuchi, Hasegawa, Tojo, and Osanai, 2008). While the development of empathy is based on the development of these other functions, it is not

surprising to find seriously impaired ability to understand and share others' beliefs and feelings.

There is overwhelming evidence that symptoms of autism result from abnormal brain development, probably as the result of genetic factors. The literature on the autistic brain was for many years marked by the scarcity and the inconstancy of the data available, probably due to the heterogeneity of the autism spectrum. Only recently, have structural and functional MRI research offered an increased understanding of the neurobiology of autism (for a complete overview see Anagnostou and Taylor, 2011; Stigler, McDonald, Anand, Saykin, and McDougle, 2011).

Anatomical studies have reported that despite normal brain size at birth in autism, rapid brain overgrowth occurs during childhood followed by a plateau meaning that the brain size is within the normal range in adulthood (Courchesne, et al., 2007; Redcay and Courchesne, 2005). Abnormalities in grey and white matter have been identified with this early brain enlargement in children with autism. Regional differences in grey matter have been found in almost all the brain areas involved in empathy (PFC, inferior frontal gyrus, STS, inferior parietal lobule, cingulate and FG as well as in the amygdala and insula (Carper and Courchesne, 2005; Carper, Moses, Tigue, and Courchesne, 2002; Hadjikhani, Joseph, Snyder, and Tager-Flusberg, 2006; Kosaka, et al., 2010; Schumann, et al., 2004). Additional abnormal characteristics of the cortex such as shape and thickness have also been reported in these brain areas (Hyde, Samson, Evans, and Mottron, 2010).

Activation of the mirror neuron system has been reported to be affected in ASD. Investigating the MNS during observation and imitation of emotional expression in children with autism, Dapretto and colleagues (Dapretto, et al., 2006) did not find any activation of the MNS in the inferior frontal gyrus and evidenced a negative correlation between MNS activation and social impairment. Underactivation of the MNS has been proposed as a crucial feature of autism spectrum disorder (Hadjikhani et al., 2006; Oberman and Ramachandran, 2007). Although confirming reduced empathic resonance in participants with Asperger syndrome, a recent study investigating the observation of another person's pain (Minio-Paluello, Baron-Cohen, Avenanti, Walsh, and Aglioti, 2009) revealed that subjects diagnosed with an Asperger syndrome seemed to code other's pain in a self-oriented manner, probably by taking an egocentric stance.

One of the first functional studies investigating the attribution of mental state in others using TEP reported that subjects with ASD recruited the same network of regions as controls when mentalizing, but showed significantly less activity in the mPFC (Happe, et al., 1996). In a nice paradigm where subjects were exposed to silent animation depicting two triangles² suggesting either a ToM condition (one triangle trying to tickle the other) or a random condition, the authors also reported reduced activation of the ToM network in the autistic group compared to controls (Castelli, Frith, Happe, and Frith, 2002). The reduced activity in the mPFC seems to be related to symptom severity in children with ASD and has been reported to be modulated by explicit instructions to attend to social information (Wang, Lee, Sigman, and Dapretto, 2007). In contrast to these previous reports, a recent study did not

² This paradigm uses basic geometric shapes. No human character, face or other human body part or emotion are used, avoiding the confusion with other social processes that have been previously reported to be affected in ASD.

observe significant hypoactivation of the ToM network in subjects with ASD (Schulte-Ruther, et al., 2011). However, there was clear dissociation of activation in the mPFC, the peak of activation being located more dorsally (DmPFC) in subjects with ASD and more ventrally in control subjects (VmPFC), confirming the different role (mentioned previously) of the ventral and dorsal portions of the mPFC (Mitchell et al., 2006). The study by Schulte-Ruther and colleagues (2011) also reported increased activation of the TPJ in ASD compared to controls, confirming the abnormal distinction between self and others (see also Minio-Paluello et al., 2009) that might contribute to a diminished ability to show contagious emotional reactions.

One important bias in the functional studies of ASD is the fact that the participants were generally high level functioning subjects and/or Asperger syndrome. As almost all the paradigms require active participation of the subjects, low level functioning subjects would not be able to achieve the task. This bias in the recruitment of subjects leads of course to bias in the interpretation of findings. Thus the data obtained could not be extrapolated to the whole spectrum, and should be cautiously restricted to HFA and Asperger syndrome.

The various reports of brain abnormalities have confirmed that autism is a distributed brain system disorder. The recent progress in neuroimaging techniques have provided evidence that these abnormalities are associated with disturbances in functional and anatomical brain connectivity (Ameis, et al., 2011; Just, Cherkassky, Keller, and Minshew, 2004; Monk, et al., 2009; for a review see Schipul, Keller, and Just, 2011). To conclude, such underconnectivity may constrain the psychological processes that rely on the integrated functioning of a distributed brain network such as empathy.

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