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Social cognition and the superior temporal sulcus: Implications in autism

Cognition sociale et sillon temporal supérieur : implications dans l’autisme

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ABSTRACT

The most common clinical sign of autism spectrum disorders (ASD) is social interaction impairment, which is associated with communication deficits and stereotyped behaviors. Based on brain-imaging results, our hypothesis is that abnormalities in the superior temporal sulcus (STS) are highly implicated in ASD. These abnormalities are characterized by decreased grey matter concentration, rest hyperperfusion and abnormal activation during social tasks. STS anatomofunctional anomalies occurring early across brain development could constitute the first step in the cascade of neural dysfunctions underlying autism. It is known that STS is highly implicated on social perception processing, from perception of biological movements, such as body movements or eye gaze, to more complex social cognition processes. Among the impairments that can be described in social perception processing, eye gaze perception is particularly relevant in autism. Gaze abnormalities can now be objectively measured using eye-tracking methodology. In the present work, we will review recent data on STS contributions to normal social cognition and its implication in autism, with particular focus on eye gaze perception.

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RÉSUMÉ

Le signe clinique le plus fréquent des troubles du spectre autistique (TSA) est un déficit dans le domaine des interactions sociales, qui est associé à des déficits de la communication et à des comportements stéréotypés. Les données en imagerie cérébrale montrent des anomalies anatomofonctionnelles au niveau du sillon temporal supérieur (STS) dans l’autisme. Ces anomalies sont caractérisées par une diminution de la concentration de la matière grise, une hyperperfusion au repos et une activation anormale lors de la réalisation de tâches sociales. Ces anomalies du STS ayant lieu très tôt dans le développement du cerveau pourraient constituer le premier élément dans la cascade de dysfonctionnements neuronaux qui

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1. Introduction

Autisme est un trouble du développement neurologique avec une gamme de présentations cliniques, allant de modéré à sévère, qui se réfère à des troubles du spectre de l’autisme (ASD). Le trouble neurodysfonctionnel le plus commun est la signification sociale de l’autisme, qui peut être observée dans l’autisme, celles de la perception du regard sont particulièrement importantes. Actuellement, ces anomalies de la perception du regard peuvent être mesurées de façon objective par la méthode d’eye-tracking. Dans la présente revue, nous présenterons les données récentes en imagerie cérébrale concernant le rôle du STS dans la cognition sociale normale et son implication dans l’autisme.

Based on brain imaging results obtained by our group and others (Ohnishi et al., 2000; Zilbovicius et al., 2000; Castelli et al., 2012; Pelphrey et al., 2011), our hypothesis is that abnormalities in the STS are highly implicated in autism (Fig. 1). Therefore, anatomical and functional anomalies in the STS occurring early across brain development could constitute the first step in the cascade of abnormal neural phenomena underlying autism (Zilbovicius et al., 2006; Kaiser et al., 2010). In this work, we will review the implication of the STS in normal and abnormal social perception processes, more specifically in eye gaze processing.

2. Social perception and social cognition: implication of the temporal lobe

The ability to recognize a specific individual within a social context is the foundation of social behavior. In less evolved mammals, this recognition is largely based on recognizing its specific individual smell. In contrast, monkeys and humans recognize individuals mostly by their facial features and by the tone of their vocalization. Consequently, our brain must have developed a specialized ability for social cognition, “the processing of information which culminates in the accurate perception of the dispositions and intentions of other individuals” (Brothers et al., 1990).

Since the end of the 1970s, studies of single cells have indicated that specialized visual mechanisms exist in the STS of non-human primates and produce selective neural responses to such things as the movement of natural images of faces and bodies (for review see Allison et al., 2000; Keysers and Perrett, 2004). In humans, nothing was known about the functions of the STS until an fMRI study published in 1996 that showed an unexpected STS activation induced by a point light display depicting a moving body (Howard et al., 1996). At the time, this was regarded as surprising, since this superior temporal lobe region was considered to be dedicated to language processing. In a PET study published in the same year, Bonda et al. (1996) demonstrated that human motion stimuli selectively activated the inferior parietal region and the STS. Since these publications a large series of papers have confirmed the implication of the STS in the perception of natural moving images of faces and bodies. STS activations were found during the perception of eye, face, mouth, hands and body movement (Zilbovicius et al., 2006; Kaiser et al., 2010; Neuhaus et al., 2010). Taken together, these studies strongly implicate the human STS and adjacent cortex in the perception of biological motion and point the STS as a key cortical

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structure for social cognition, suggesting that the initial analysis of visual social cues, called social perception, occurs in the STS (Allison et al., 2000).

Since then, new data implicating the STS in social cognition were published and have enlarged our knowledge about the role of the STS in this process. STS has been implicated in social auditory perception as well as in gaze perception and in analysis and interpretation of the intention of other’s, known as ToM.

Regarding social auditory perception, dedicated neural territories that selectively respond to voices rather than to other natural sounds were found along the STS (Belin et al., 2000). Preferential responses to voices have been observed in regions along both STS with a right hemispheric predominance (Belin et al., 2000; Belin and Zatorre, 2003). Recognition of both familiar and non-familiar voices has also been found to activate the posterior STS (Kriegstein and Giraud, 2004). In addition, there is increasing evidence that the STS also processes auditory action related information. For example, Bidet-Caulet et al., 2005 reported activity in the STS as participants listened to footsteps. Other studies have shown greater STS activity to hearing human actions, such as yawning or chewing, compared to hearing other environmental or mechanical actions (Lewis et al., 2011).

In social visual cognition, gaze is undoubtedly special, perhaps without a match in its significance as a biological signal. In a series of studies, Pelphrey et al., 2004a,b have investigated the degree to which STS activation is modulated by the context of the perceived eye movement. For example, they studied STS activation during eye gaze perception when gazes shift correctly or incorrectly towards a visual target, or whether the eye gaze conveys the intention to engage in or withdraw from a social interaction. They have showed that the STS is sensitive to the social context within which a gaze shift occurs, i.e. whether the gaze is perceived to be consistent or inconsistent with the subject’s expectation regarding the intention of the person making the eye movement (Pelphrey et al., 2004a). In that study, which used a functional MRI (fMRI) paradigm with typically developing subjects, a strong effect of context was observed in the right posterior STS region in which observation of gaze shifts away from a target (incongruent shifts) evoked a haemodynamic response with extended duration and greater amplitude compared with gaze shifts toward the target (congruent shifts). In a similar study from the same group, also performed in typically developing subjects, the STS showed a greater response when participants viewed a reach gesture incongruent with a prior emotional expression than when they viewed a reach gesture congruent with the prior expression, regardless of whether expectations were induced by a positive or a negative emotional expression (Wyk et al., 2009). Consistent with prior studies, the STS, the middle temporal gyrus, and inferior parietal lobule were sensitive to the intentions underlying the stimulus character’s eye movements. It has also been demonstrated that the STS region plays a critical role in processing eye gaze signals of approach and avoidance (Pelphrey et al., 2004b) and it responds to the intentionality of other observed human actions including reaching-to-grasp movements of the arm and hand (Pelphrey et al., 2004a).

Research has demonstrated that STS responds to specific aspects of social gestures, including “the intentionality and appropriateness of biological motion” (Pavlova et al., 2008;
Wyk et al., 2009; Thompson and Parasuraman, 2012). Therefore, STS activation has also been reported in response to possible versus impossible human movements (Stevens et al., 2000), as well as meaningful vs. non-meaningful hand motions (Decety et al., 1997). These data indicate that STS processing is concerned with more than just perceptual aspects of moving or movable body parts. Rather, networks in this brain region may analyze gaze and other movements to the extent that these cues meaningfully contribute to social communication. These findings suggest that achieving joint attention, a pivotal skill in social cognition, is facilitated by the analysis of sensory cues in the STS.

In addition, studies have shown that temporal structures are also involved in more complex aspects of social interaction such as the ToM. Castelli et al. (2000) and Schultz et al. (2004) reported that the STS showed a significantly higher response to animations of moving geometric shapes that depicted complex social interactions than to animations depicting random motion. Using movies of human actors engaged in structured goal-directed actions (e.g. cleaning the kitchen), Zacks et al., 2001 found that activity in the STS was enhanced when the agent switched from one action to another, suggesting that this region encodes the goal-structure of actions. These results indicate that the STS is also implicated in representing intentional action, and not only in perception of biological motion.

There is great overlap between the posterior temporal regions identified by ToM and gaze studies. It is clear that the region of posterior temporal cortex (i.e. the STS) that Haxby et al., 2002 associated with the visual analysis of changeable aspects of the face (i.e. gaze, emotional expressions, mouth movements, etc.), is very similar to the regions engaged by ToM tasks.

More recently, researchers have been interested in the continuum between normal and pathological neural system regarding social perception. Interestingly, these studies show an association between individual scores in sociability scales and anatomo-fonctional aspects of the STS. Brain imaging studies performed in the general population have been using scales of social adaptability or autistic traits scales (Baron-Cohen et al., 2001) to establish a continue line of the social functioning degree in normal people. These studies have shown, for instance, that scores of autistic traits in normal population are associated with cortical thickness in several regions of the social brain, particularly along the STS: the higher the scores indicating the presence of autistic traits in normal population are, the thinner the cortex is in these areas (Wallace et al., 2012). A different study, also performed in the general population, used VBM (voxel based morphometry) analysis and showed a significant decrease in white matter volume associated with the increased of scores of autistic traits in only one region: the right posterior STS. Further than that, increased cortical response to changes in gaze direction occurred in the pSTS are predicted by scores of autistic traits in typical adults (von dem Hagen et al., 2011). Anecdotally, significant correlation has been described between grey matter density in the right STS and the number of friends a person has in an online social network: the more friends the person has, the higher the grey matter density is in this area (Kanai et al., 2012). These and other findings support more and more the STS implication in social perception and social cognition.

3. Social perception and social cognition: from typical development to autism

The capacity to identify biological agents from non-biological ones plays a critical role in the process of adaptive behavior. Several studies have demonstrated that, from a very early stage in development, the human visual system is particularly sensitive to biological motion (Jones et al., 2008; Klin et al., 2009; Bardi et al., 2011). Visual processing of biological motion produced by living organisms is of immense value for successful daily-life activities and, in particular, for adaptive social behavior and nonverbal communication (Pavlova, 2012). From the very first hour of life human newborns give preferential attention to people, and this tendency persists during development. At four-day-old, they distinguish between a face looking toward them and a face looking away; by three months-old, infants look more at a person’s eyes than at other parts of the face; by four months of age, infants exhibit a visual preference for upright over upside-down point light figures (Klin et al., 2003; Senju et al., 2008). This is evidence, from a very early stage in development, of a preferential processing of social information among different stimuli. This preferential processing will be the foundation for the development of what may be called a “social expertise”, which will play a major role in the subsequent development of all social interaction processes (Fridh and Frith, 2012).

Making eye contact is the most powerful mode of establishing a communicative link between humans (Farroni et al., 2002). Among the most striking social impairment symptoms in ASD are deficits in joint attention and in using information concerning eye gaze to understand other’s mental states and intentions, both of which rely on social perception process (Fridh et al., 1991; Baron-Cohen et al., 1994; Klin et al., 2003). “I had no idea that other people communicated through subtle eye movements,” says an adult with autism, “until I read it in a magazine five years ago”. Such a capacity may be a prerequisite for higher level appreciation of the minds of others and is part of this larger cognitive domain called ToM or social cognition, which is severely impaired in autism (Fridh et al., 1991; Baron-Cohen et al., 1999). Indeed, individuals with autism have deficits in the perception of eye gaze, poor eye contact during communication, and difficulties accessing information to infer the mental state of others (Klin et al., 2003).

4. Eye gaze abnormalities in autism: eye tracking studies

In the last decade, the use of eye-tracking methodology has allowed a better characterization of the social perception deficits in autism, particularly a lack of preference for the eyes. This methodology allows to objectively analyze gaze pattern during the viewing of naturalistic situations or during the performance of cognitive tasks. Studies where adults and children with autism were presented with a naturalistic social
scene have shown that they have a preference for non-social information (physical details of the environment) rather than for the social information (faces and eyes of characters) that is presented (Klin et al., 2002; Speer et al., 2007; Jones et al., 2008; Chawarska and Shic, 2009). In 2002, Klin et al. have shown that high functioning adults with ASD looked less to the eyes of characters and more to mouths and physical details in a movie than did matched controls. In children, a lack of preference for biological motion has also been shown in a number of studies (for review see Boraston and Blakemore, 2007; Falck-Ytter and von Hofsten, 2011). For example, two years-old toddlers with autism have shown no preference for point-lights biological motion, contrary to typically developing controls (Klin et al., 2009). Children with autism also showed a preference for geometric patterns of movement rather than for social movement (Pierce et al., 2011). They will also look less to eyes and face areas and more to body and objects when watching scenes from a movie (Rice et al., 2012).

Interestingly, a recent study from our team has allowed to show that gaze pattern in children with autism varies according to the type of stimuli that is used. Indeed, when presented with four different types of stimuli (real characters movie, cartoon movie, real characters pictures and cartoon pictures) children with autism look less to the eyes in the situation that is more ecologically relevant (real characters movie) than in cartoons when compared to controls (Fig. 1) (Saitovitch et al., submitted).

Abnormalities in gaze pattern have also been shown in subjects with autism while performing different tasks. Adults with autism have shown impairments in emotion recognition when presented with human pictures. The lower performance is this task was associated with abnormal visual strategy in face exploration (Pelphrey et al., 2002). This kind of impairment has also been described in children with autism, who were slower than controls to recognize emotions from human pictures. In this study, better emotion recognition in the autistic group was associated with increased gaze to the eyes region (Bal et al., 2010).

These results from eye-tracking studies show in an objective way the presence of abnormalities in the processing of visual social information in autism, which could underline the comprehension of more complex social situations. They also suggest a link between behavioral symptoms and brain networks abnormalities that seem to be implicated in autism.

In addition, Zilbovicius et al., 2000 performed an individual analysis of their data comparing each autistic child to the control group. They detected individually a significant temporal hypoperfusion in 16 of the 21 autistic children (77%). Moreover, a replication group study was performed in an additional group composed of 12 autistic children and confirmed both group and individual results (Zilbovicius et al., 2000). Thus, the bitemporal hypoperfusion was confirmed in three independent groups of autistic children and provided the first robust evidence for temporal lobe dysfunction in school-aged children with autism.

New methodology in brain imaging analysis using whole brain multivariate classification developed in our team have allowed the detection of individual significant temporal hypoperfusion in children with ASD participating in the studies described above (Duchesnay et al., 2011). The classification rate was of 88% of individual detection (51 correct classification over 58 subjects), with a 91% rate of sensibility (41 correct classifications over 45 ASD subjects) and a 77% rate of specificity (10 correct classifications over 13 control subjects).

In another study, a correlation analysis was performed in order to investigate a putative relationship between regional rest cerebral blood flow (rCBF) and the clinical profile of 45 autistic children. Autistic behavior was evaluated with the Autism Diagnosis Interview (ADI-R) (Lord et al., 1994). Significant negative correlation was observed between rCBF and the ADI-R score in the left superior temporal gyrus. The higher the ADI-R score (the more severe autistic syndrome is), the lower rCBF is in this left temporal region (Gendry Meresse et al., 2005).

5.2. Anatomical MRI data

Quantitative structural imaging studies have benefited greatly from both new technologies for data acquisition and new image analysis approaches. Using parametric mesh-based analytic techniques, Levitt et al., 2003 showed significant differences in cortical sulcal patterns in children with autism localized mainly in the frontal and temporal sulci. By using a direct measurement of cortical thickness to examine the gray matter integrity and to explore the anatomical substrate of behavioral symptoms of ASD, Hadjikhani et al., 2006 found local decreases of the gray matter in the ASD group in the inferior frontal gyrus, in the inferior parietal lobule and in the STS. In addition, cortical thinning in these regions was correlated with ASD symptom severity.

A pioneering study in ASD using voxel based morphometry (VBM) was published in 1999 by Abell et al. (1999) and showed fronto-temporal gray matter abnormalities. Since then, VBM has benefited from substantial methodological improvements. We performed a MRI study using VBM and high-resolution 3D-T1-weighted images acquired from 21 children with autism and 12 healthy control children. We found significant bilateral decreases of grey matter in the STS of children with autism (Boddaert et al., 2004). The major finding of this study was the remarkable consistency between the bilateral temporal abnormalities found in autistic children by three independent MRI, PET (Zilbovicius et al., 2000) and SPECT studies (Ohnishi et al., 2000). A more recent study performed in
children with autism compared to controls showed that children with autism had reduced grey matter volumes in brain regions with critical socio-emotional function, such as the right fusiform gyrus and the STS (McAlonan et al., 2005).

The white matter structure also seems to be altered in subjects with autism when compared to controls. For instance, Barnea-Goraly et al. (2010) have used Diffusion Tensor Imaging (DTI) to investigate white matter structural integrity in children and adolescents with autism. Based on voxel-wise analysis, they found reduced FA (fractional anisotropy) values in brain regions that were implicated in theory-of-mind tasks (ventromedial prefrontal cortex, anterior cingulate, temporoparietal regions, amygdala), and in social cognition (fusiform gyrus and adjacent to STS). Investigation of possible correlations between autistic symptoms and brain structure also point to an implication of abnormal anatomical connectivity in autism (Just et al., 2004). Anatomo-clinical correlations were mainly found in inferior frontal and superior temporal white matter regions, through which two main bundles, the arcuate and the uncinate fascicule pass (Mori et al., 2008). In a recent study developed in our lab, we investigated the correlation between autism severity, measured by the ADI-R (Lord et al., 1994), and diffusion MRI parameters in children and adolescents with autism. Results showed that ADI scores correlated with FA decrease in superior temporal and frontal inferior white matter regions (Bargiacchi et al., submitted).

### 6. Activation PET and MRI studies

Studies using fMRI have relied on different paradigms related to social processes to investigate differences in brain activity between subjects with autism and control subjects during performance of variable tasks (for review see Philip et al., 2011). In a study developed in our lab, fMRI results point out the absence of activation of the “voice-selective area” in autism (Gervais et al., 2004). We found significant differences in brain activation during voice perception among individuals with autism compared to normal controls. In normal controls, listening to voice compared to non-voice significantly activated a “voice-selective area” located bilaterally along the upper bank of the STS (Belin et al., 2000). Voice perception in the autistic group did not yield activation of any other brain region relative to non-voice perception. In the autistic group, listening to voice and to non-voice sounds activated the same primary auditory regions. In addition, unlike the individual data obtained in controls, all but one autistic subject failed to activate the “voice-selective area”. The absence of activation of the “voice-selective area” in the autistic group was also confirmed by a direct comparison of the two groups’ activation maps. The acoustic structure of the voice contains a lot of socially relevant information, such as identity and emotional state; so, we present evidence for difficulty in social perception in auditory world.

The processing of faces in individuals with autism appears to be atypically organized in comparison to the network observed in control subjects. Activations in the fusiform face area (FFA) (Haxby et al., 2002), and the occipital face area are commonly reported as reduced in individuals with ASD (Philip et al., 2011). Schultz et al. (2000) were the first to use fMRI to study face perception in autistic subjects. They found a significantly less activation of the middle aspect of the right FFA in 14 high functioning individuals with ASD compared to controls (Schultz et al., 2000). Hypoactivation of the FFA was replicated in a series of functional studies (Critchley et al., 2000; Pierce et al., 2001; Hubl et al., 2003). In the same vein, Critchley et al., 2000 investigated whether high functioning individuals with ASD showed a different pattern of cortical activation when processing facial expressions. Nine autistic adults and nine age-matched controls were asked to perform explicit (conscious) and implicit (unconscious) identification of emotional facial expressions. Autistics differed significantly from controls in the activation of the cerebellum, the mesolimbic, and temporal lobe cortical regions when observing facial expressions (consciously as well as unconsciously). Notably, they didn’t activate a cortical FFA when explicitly appraising expressions (Critchley et al., 2000).

In a study investigating mentalization process, Castelli et al., 2002 have studied cortical activation enhanced by animation of geometric figures. The animations depicted two triangles moving around on a screen in three different conditions: moving randomly, moving in a goal-directed fashion (chasing, fighting), and moving interactively with implied intentions (coaxing, tricking). The last condition frequently elicited descriptions in terms of mental states that viewers attributed to the triangles (mentalizing). Ten adults with ASD and 10 control adults were scanned while watching animated sequences. The ASD group gave fewer and less accurate descriptions of the mentalizing animations, but equally accurate descriptions of the other animations compared with controls. While viewing animations that elicited mentalizing (as opposed to randomly moving shapes) the control group showed increased activation in a previously identified mentalizing network (medial prefrontal cortex, STS and temporal poles). The ASD group showed less activation than the control group in all these regions. However, one additional region, the extrastriate cortex, which was highly active when watching animations that elicited mentalizing, showed the same amount of increased activation in both groups. In the autism group this extrastriate region showed reduced functional connectivity with the STS (Castelli et al., 2002).

Pelphrey et al., 2005 also found abnormal STS activation during an eye gaze perception task in autistic adults. On congruent trials, subjects watched as a virtual actor looked towards a checkerboard that appeared in her visual field, confirming the subject’s expectation regarding what the actor ‘ought to do’ in this context. On incongruent trials, she looked towards empty space, violating the subject’s expectation. In normal subjects incongruent trials evoked more activity in the STS and other brain regions linked to social cognition, indicating a strong effect of intention. The same brain regions were activated during observation of gaze shifts in subjects with autism, but did not differentiate congruent and incongruent trials, indicating that activity in these regions was not modulated by the context of the perceived gaze shift. These results indicate a difference in the response of brain regions underlying eye gaze processing in autism. The authors suggested that the lack of modulation of the STS region by
gaze shifts that convey different intentions contributes to the eye gaze processing deficits associated with autism. These results were replicated in a similar study by the same group, with a different set of participants. As previously described, typical developing controls showed an incongruent greater than congruent effect in the activation of the right posterior STS. Subjects with autism did not present this incongruent greater than congruent effect, showing no difference in brain activation in the congruent or incongruent situations (Pelphrey et al., 2011).

7. General conclusion

Researches developed over the last decade have helped to better characterize the major impairments in social cognition that consist the core characteristic of autism. On the behavioral level, thanks to new methodologies such as eye tracking, we have a better understanding of how autistic subjects perceive the world around them. A general lack of preference for biological motion and social stimuli, which can be found very early in typical development, has been systematically described. More particularly, a lack of preference for the eyes is a key feature in social cognition impairments associated to autism. On the brain level, several studies have found anatomical and functional abnormalities in autism, particularly located on the STS. These STS abnormalities are characterized by decreased grey matter concentration, rest hyperperfusion and abnormal activation patterns during social cognition tasks. The STS is known to be a critical region for social cognition and is implicated in several steps of social interactions: from auditory and visual social perception (voice, gestures, facial displays of emotions and eye gazes perception) to more complex social cognition processes (ToM and mentalizing). In addition, the STS is also highly connected with other regions of the social brain such as the FFA, the orbito-frontal cortex and the amygdala. All these regions were found to be abnormally activated in ASD during tasks implicating social cognition.

The data reviewed in this paper suggest that abnormalities in the STS could be the first step in the cascade of abnormal neural phenomena underlying autism. These early development mental abnormalities of the STS would lead to abnormal connectivity among key regions of the social brain in autism, which could be account for the observed abnormalities in social perception and social cognition processes. These data provide new outlook into the understanding in ASD, arguing for a deficit in the perception of socially relevant stimuli. Thus, it could help to develop new therapeutical approaches, focusing on social perception process, mainly early gaze interaction, to stimulate the development of a “social expertise” and to improve social cognition in autism.

Disclosure of interest

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