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Autism, the superior temporal sulcus and social perception

Monica Zilbovicius[1], Isabelle Meresse[1,2], Nadia Chabane[3], Francis Brunelle[4], Yves Samson[2] and Nathalie Boddaert[1,4]

[1]URM 0205 Brain Imaging in Psychiatry, INSERM-CEA, Service Hospitalier Frédéric Joliot, CEA, 4 Place du General Leclerc, Orsay 91406, France
[2]Service des Urgences Cerebro-Vasculaires, Groupe Hospitalier Pitié-Salpêtrière, AP-HP, 47 Bl. de l'Hôpital, Paris 75013, France
[3]Service de Pédopsychiatrie, Hôpital Robert Debré, AP-HP, 48 Bl. Serurier, Paris 75019, France
[4]Hôpital Necker Enfants Malades, AP-HP, Paris V, 149 Rue de Sevre, Paris 75007, France

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 recent brain-imaging results, our hypothesis is that abnormalities in the superior temporal sulcus (STS) are highly implicated in ASD. STS abnormalities are characterized by decreased gray matter concentration, rest hypoperfusion and abnormal activation during social tasks. STS anatomical and functional anomalies occurring during early brain development could constitute the first step in the cascade of neural dysfunction underlying ASD. We will focus this review on the STS, which has been highly implicated in social cognition. We will review recent data on the contribution of the STS to normal social cognition and review brain-imaging data implicating this area in ASD. This review is part of the *INMED/TINS* special issue *Nature and nurture in brain development and neurological disorders*, based on presentations at the annual *INMED/TINS* symposium (http://inmednet. com/).

Introduction

Autism is a neurodevelopmental disorder with a range of clinical presentations, from mild to severe, referred to as autism spectrum disorders (ASD). The most common clinical ASD sign is social-interaction impairment, which is associated with verbal and non-verbal communication deficits and stereotyped obsessive behaviors [1]. Thanks to recent brain-imaging studies, scientists are getting a better idea of the neural circuits involved in ASD. Brain-imaging studies have also enabled a better understanding of the neural circuits involved in normal human social interaction. They have identified brain regions involved in social perception and the networks underlying theory of mind (analysis and interpretation of the intentions of others) [2], which are both impaired in ASD. As defined by Allison *et al.*, social perception refers to initial stages in 'the processing of information which culminates in the

accurate analysis of the dispositions and intentions of other individuals' [2]. At the end of the 20th century, if we had asked most neuroscientists about the 'social brain' they would have immediately identified the frontal lobe and limbic system, and more specifically structures such as the orbitofrontal cortex, the amygdala and the striatum. These structures are indeed deeply involved in mood, motivation and decision processing. More recently, researchers have also focused on another aspect of the social brain, which can broadly be called 'social perception', in which it is now clear that the superior temporal sulcus (STS) is a major player. Therefore, Brothers *et al.* [3] proposed that the amygdala, the orbitofrontal cortex (OFC), inferotemporal face-responsive regions and the STS represent areas primarily involved in the processing of socially relevant information. Adolphs [4] extended this proposal by differentiating between higher-order sensory cortices such as the fusiform gyrus and superior temporal sulcus, which are involved in detailed perceptual processing, and the amygdala, ventral striatum and orbitofrontal cortex, which link sensory representations of stimuli to their motivational value.

Based on recent brain-imaging results obtained for ASD [5–14], abnormalities in the STS are strongly implicated in ASD. Therefore, anatomical and functional anomalies in the STS during early brain development could constitute the first step in the cascade of abnormal neural phenomena underlying ASD. We will focus this review on the STS, which has been strongly implicated in social perception and more specifically in eye-gaze processing. Indeed, two of the most striking social impairments in ASD are deficits in joint attention (being directed to observe an event by following the eye gaze or pointing gestures of another individual) and in using information concerning eye gaze to understand others' mental states and intentions [15,16].

In a seminal review about the role of the STS in social perception, Allison *et al.* stated that it is plausible that there are STS anomalies in autism, although they also pointed out that there were 'no studies specifically implicating the STS region in autism' [2]. Five years later, new brain-imaging techniques enabled Dakin and

Corresponding author: Zilbovicius, M. (mozilbo@gmail.com).

Frith to suggest that 'abnormalities in the STS may provide a neural basis for the range of motion processing deficits observed in ASD, including biological motion perception' [17]. They went on to say that, 'such an explanation may also provide a link between perceptual abnormalities and specific deficits in social cognition associated with autism'. In the present paper, we will briefly review data about the STS contribution to social cognition that were published after the article of Allison *et al.* [2], and then review brain-imaging data implicating the STS in ASD.

The social brain: the new role of the temporal lobe
The ability to recognize a specific individual within a social context is the foundation of social behavior. In non-primate mammals, recognition of a specific individual is based largely on recognizing its specific individual smell. By contrast, monkeys and humans recognize individuals mostly by their facial features and the tone of their vocalizations. Consequently, our brain must have developed a specialized ability for social cognition [3].

Since the end of the 1970s, studies of single cells have indicated that specialized visual mechanisms in the STS of non-human primates produce selective neural responses to such things as the movement of natural images of faces and bodies [2,18]. In humans, nothing was known about the functions of the STS [19] until Howard *et al.* published a functional magnetic resonance imaging (fMRI) study in 1996 showing unexpected STS activation induced by a point-light display depicting a moving body [20]. At the time, this was regarded as surprising because this superior temporal lobe region was considered to be dedicated to auditory processing of speech sounds. A positron emission tomography (PET) study published in the same year by Bonda *et al.* [21] demonstrated that human motion stimuli selectively activated the inferior parietal region and the STS. Since these publications, many papers further implicated the STS in the perception of moving natural images of faces and bodies. STS activation was found during the perception of eye, face, mouth, hand and body movement [22–33]. Together, these studies strongly implicate the human STS and adjacent cortex in the perception of body movements of other individuals; they led Allison *et al.* to point to the STS as a key cortical structure for social cognition and to suggest that the initial analysis of visual social cues, called social perception, occurs in the STS [2,22–33]. Since then, new data have expanded our knowledge about the role of the STS in social cognition, implicating it in two main domains: (i) auditory social perception, based largely on evidence from voice perception studies [34–36]; and (ii) in more complex social cognition, particularly in theory of mind [37–45].

Voice perception – a social perception in the auditory world
The human voice is probably the most important sound category of our auditory environment. Evidently, it carries speech, which makes humans a unique species. Voices are also an 'auditory face', rich in information concerning the identity and affective state of the speaker [34]. Humans

can extract this information – sometimes to a surprising degree – and consequently form representations in long-term memory that enable us to recognize voices on the telephone, for example. Although these 'vocal cognition' skills have a fundamental role in social interaction, little is known about the underlying cerebral mechanisms.

Research suggests that vocal cognition involves voice-selective regions of the auditory cortex located along the STS, analogous to the 'face areas' of the visual cortex, and possibly organized in functionally distinct cortical pathways [34,35]. Dedicated neural territories that selectively respond to voices rather than to other natural sounds are located along both superior temporal sulci [34], with a right hemispheric predominance [34–36]. Recognition of both familiar and non-familiar voices has also been found to activate the posterior STS [36]. In this voice-recognition study, Kriegstein and Giraud delineated three distinct areas along the right STS involved in different aspects of voice processing. These areas respond and interact differentially depending on (i) acoustic information of the speech stimulus, (ii) the specific task, and (iii) the familiarity with the speaker. The mid-anterior STS carry out a spectral analysis of voices. More posterior and anterior areas emphasize voice processing over linguistic analysis of speech sounds and are both functionally connected to the mid-anterior area during voice recognition. However, the anterior and posterior areas show different response properties: the anterior area responds specifically to voice recognition whereas the posterior area shows a less-specific role in voice processing – that is, sensitivity to the temporal complexity of sounds including non-vocal and non-linguistic sounds. Whereas recognition of familiar voices predominantly modulates connectivity between the anterior STS and the medial temporal lobe memory system, recognizing non-familiar voices predominantly involves functional interactions between bilateral mid-anterior and posterior STS regions, and of these regions with a frontoparietal network [36].

Complex social cognition: analysis and interpretation of the intention of others
Activation of the STS in subjects presented with images of humans making movements is greater when the movements are physically possible than when they are impossible [37]; activation of the STS is also greater in response to meaningful hand motions than in response to non-meaningful ones [33]. These data thus indicate that STS processing is concerned with more than just perceptual aspects of moving or movable body parts. Rather, networks in this brain region might 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.

Studies have also shown that temporal structures are involved in more complex aspects of social interaction, such as the theory of mind. First, Castelli *et al.* [38] and Schultz, *et al.* [39] reported that the STS showed a significantly greater response to animations of moving geometric shapes that depicted complex social interactions than to
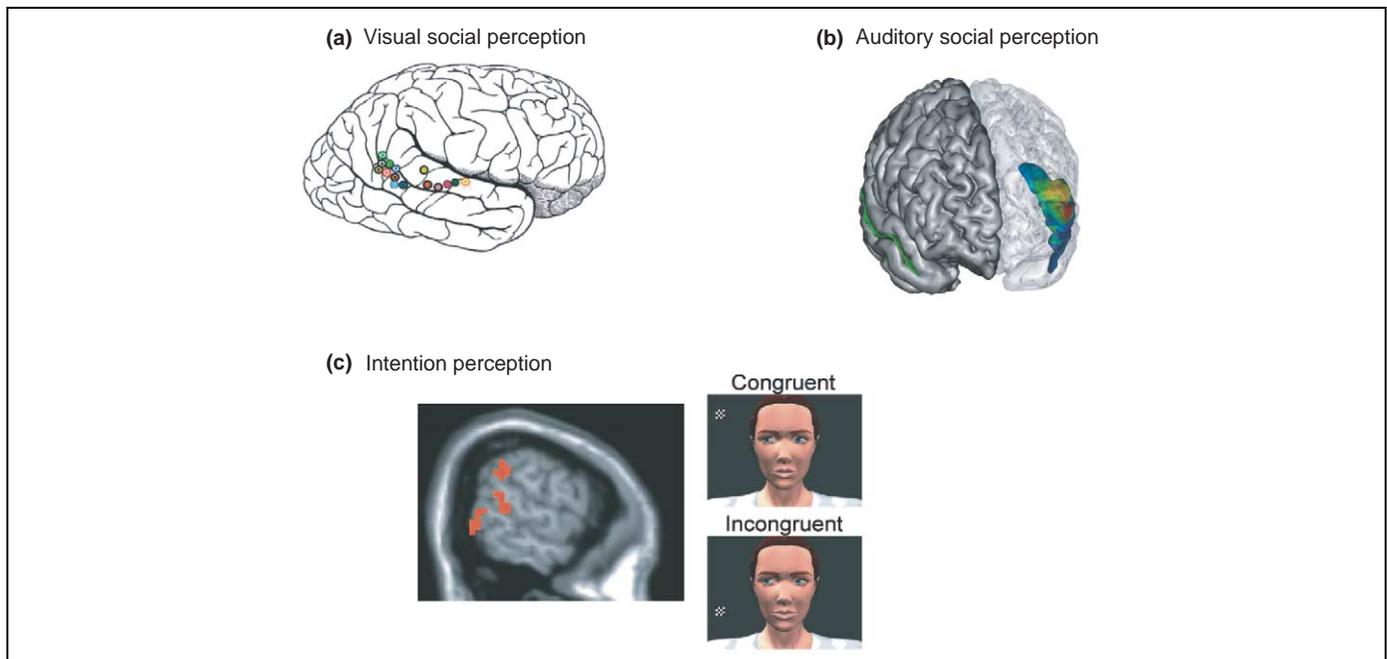
Figure 1. Summary of the most representative results from functional brain imaging that implicate of the superior temporal sulcus (STS) in different aspects of social cognition. **(a)** Results implicating the STS in visual social perception. Each colored dot located along the STS represents activation of that area in a study of perception of eye gaze, hand movement, body movement and mouth movement. Adapted from Ref. [2]. **(b)** Results implicating the STS in perception of the human voice. Colored areas are those activated during listening to a human voice compared with listening to non-vocal sounds. Adapted from Refs [34,35]. **(c)** Results implicating the STS in more complex aspects of social cognition, for example the understanding of intentions of other people. The activation map indicates regions in which response to incongruent eye gaze (when the character shifted her gaze towards empty space) was greater than that to congruent gaze (when the character shifted her gaze towards the checkerboard). These regions include the STS, implicating the STS in the understanding of gaze shifts that convey different intentions. Adapted from Ref. [45].

animations depicting random motion. Second, using movies of human actors engaged in structured goal-directed actions (e.g. cleaning the kitchen), Zacks *et al.* [40] 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. All of these results are consistent with a role for a region of the STS cortex in representing intentional action and mentalizing (i.e. making inferences about mental states), and not in just biological motion.

Finally, in a recent series of studies, Pelphrey and colleagues [44,45] 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 an eye-gaze perception when gazes shift correctly and incorrectly to 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 – that is, 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 [44]. In that study, which used an fMRI paradigm and neurologically normal subjects, a strong effect of context was observed in the right posterior STS region: observation of shifts of gaze away from a target (incongruent shifts) evoked a haemodynamic response with longer duration and greater amplitude than did gaze shifts towards the target (congruent shifts). Pelphrey and colleagues have also demonstrated that the STS region is crucial in processing eye-gaze signals of approach and avoidance [45]. The STS

also responds to the intentionality of other observed human actions, including reaching-to-grasp movements of the arm and hand, and is sensitive to the level of intentionality exhibited by simple geometric figures moving in a goal-directed manner [45]. These and other findings support the conclusion that the human STS is involved in social perception and social cognition via the visual analysis of social information conveyed by gaze direction, body movement and other types of biological motion (Figure 1).

Temporal lobe abnormalities in autism: new brain imaging findings

Children 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. 'I had no idea that other people communicated through subtle eye movements,' said an adult with autism, 'until I read it in a magazine five years ago.' Such a capacity might be a prerequisite for higher-level appreciation of the minds of others and is part of the larger cognitive domain of theory of mind and social cognition, which is severely impaired in autism [46,47].

Rest functional PET and SPECT data
Recently, PET and single-photon emission computed tomography (SPECT) studies have described localized bilateral temporal hypoperfusion in children with autism. These rest functional abnormalities were centered in the STS and superior temporal gyrus [5,6]. In both studies, autistic and control groups were matched for age and developmental quotients. Children with idiopathic mental
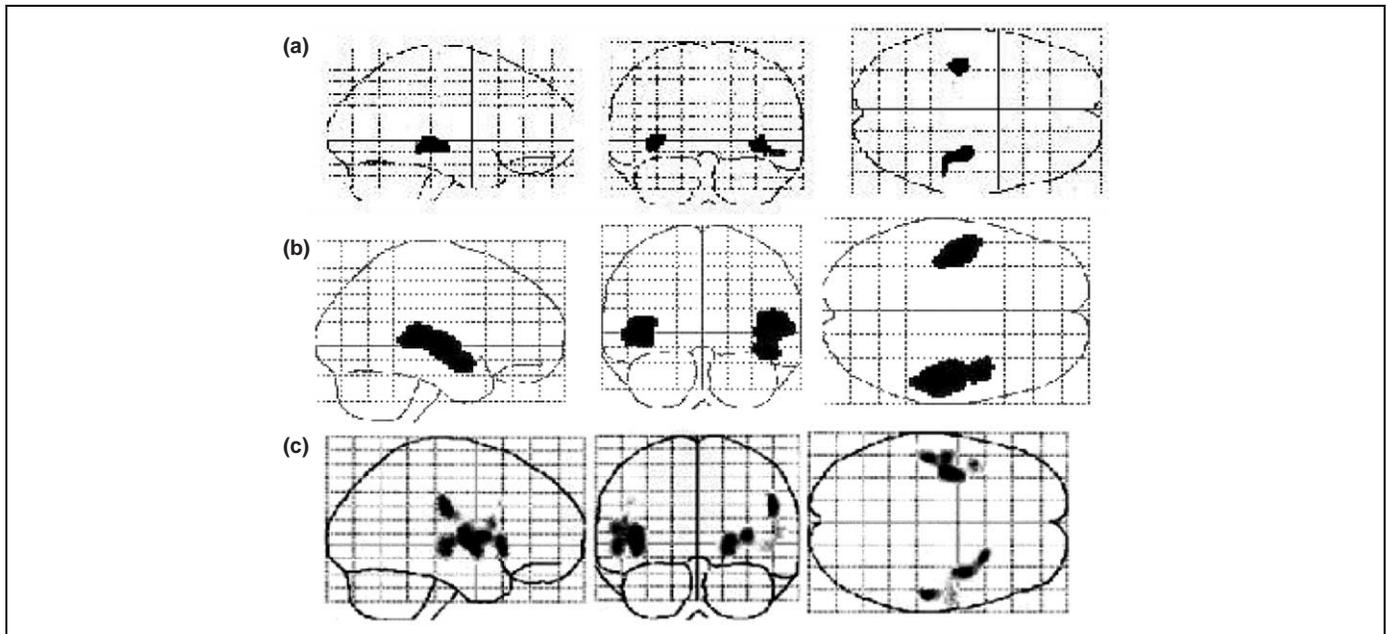
Figure 2. Results from anatomical MRI and rest functional brain-imaging studies have revealed STS anomalies in children with autism spectrum disorders (ASD). In these sagittal, coronal and axial (from left to right) views of the brain, black regions are those that differ significantly in concentration of gray matter (as measured by MRI **(a)** [11]) and in rest regional blood flow (as measured by PET **(b)** [5] and SPECT **(c)** [6]) in children with ASD when compared with non-ASD children. Theses three studies have used the same image analysis software (statistical parametric mapping, SPM). The black areas contain the STS regions.

retardation constituted control groups so the findings could not be attributed to the mental retardation.

In addition, Zilbovicius *et al.* performed an individual analysis of their data comparing each autistic child to the control group [5]. Individually, significant temporal hypoperfusion was found in 16 of the 21 autistic children (77%). Moreover, a replication-group study was performed on an additional group of 12 autistic children, and this confirmed both group and individual results [5]. 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.

Correlation analysis has also recently been used to investigate a putative relationship between regional rest cerebral blood flow (rCBF) and the clinical profiles of 45 autistic children. Autistic behavior was evaluated using the Autism Diagnosis Interview (ADI-R). Significant negative correlation was observed between rCBF and the ADI-R score in the left superior temporal gyrus. The higher the ADI-R score (i.e. the more severe the autistic syndrome), the lower the rCBF in this left temporal region [7].

Anatomical MRI data
Recently, 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.* [8] showed that cortical sulcal patterns were significantly different in control children and children with autism, and that these differences were mainly in the frontal and temporal sulci. 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.* found local decreases of gray matter thickness in the ASD group in the inferior frontal gyrus, inferior parietal lobule and STS [9]. In addition, cortical thinning in these regions correlated with ASD symptom severity.

New whole brain analysis methods have also intensely improved during the past few years. Voxel-based morphometry (VBM) provides a voxel-wise assessment of regional gray and white matter abnormalities in the whole brain without an a priori hypothesis about their localization. A pioneering study of ASD using VBM by Abell *et al.* in 1999 [10] showed frontotemporal gray-matter abnormalities. Since this publication, VBM has benefited from substantial methodological improvements. In an MRI study using VBM and high-resolution 3D-T1-weighted images acquired from 21 children with autism and 12 healthy control children, there were significant bilateral decreases of gray-matter thickness in the STS of children with autism [11]. The major finding of this study was the remarkable consistency with the bilateral temporal abnormalities found in autistic children by independent MRI [11], PET [5] and SPECT [6] studies (Figure 2).

Activation PET and MRI studies
Face perception
Schultz *et al.* were the first to use fMRI to study face perception in autistic persons. They found significantly less activation of the middle aspect of the right fusiform face area (FFA) than in controls [48] in 14 high-functioning individuals with ASD. Hypoactivation of the FFA was replicated in a series of functional studies [48–52]. In the same vein, Critchley *et al.* investigated whether high-functioning people with ASD showed a different pattern of cortical activation when processing facial expressions [50]. 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 activation of the cerebellum and of mesolimbic and temporal lobe cortical regions when observing facial expressions (both consciously and unconsciously). Notably, their cortical FFAs were not activated when explicitly appraising expressions. Hubl *et al.* showed FFA hypoactivation in seven adult males with autism, using both gender discrimination and a neutral versus expressive discrimination task [51].

Voice perception

Recent fMRI results point out the absence of activation of the 'voice-selective area' in autism, agreeing with previous functional data highlighting abnormal face processing in autism. Brain activation was found to be significantly different during voice perception among individuals with autism compared with normal controls [12]. In normal controls, listening to voice compared to non-voice sounds significantly activated a voice-selective area located bilaterally along the upper bank of the STS. Voice perception in the autistic group did not activate any other brain region any more than non-voice perception did (Box 1). In the autistic group, listening to voice and to non-voice sounds activated the same primary auditory regions. In addition, in contrast to 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 was also confirmed by a direct comparison of the two groups' activation maps [12]. The acoustic structure of the voice contains much socially relevant information, such as identity and emotional state, so these findings

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Box 1. STS and abnormal social cognition in ASD

Various brain-imaging studies have showed abnormal or absent superior temporal sulcus (STS) activation in subjects with autism spectrum disorders (ASD) during tasks involving social cognition.

In their studies, Castelli *et al.* [13] used animated geometric figures. The animations depicted two triangles moving about on a screen in three different conditions: (i) moving randomly, (ii) moving in a goal-directed fashion (chasing or fighting), and (iii) moving interactively with implied intentions (coaxing or tricking). The third condition frequently elicited descriptions in terms of mental states that viewers attributed to the triangles. While viewing animations that elicited such mentalizing, the normal group showed increased activation in the mentalizing network, including the STS (Figure Ia). The ASD group showed less activation than the normal group in all these regions.

Using functional magnetic resonance imaging (fMRI), Gervais *et al.* [12] showed that individuals with autism failed to activate STS voice-selective regions in response to vocal sounds, whereas they showed a normal activation pattern in response to non-vocal sounds (Figure Ib). These findings suggest abnormal cortical processing of socially relevant auditory information in ASD.

Consistent with a prior report from their laboratory that used the same eye-gaze task in neurologically normal subjects, Phelphrey *et al.* [14] showed that incongruent trials evoked more activity than congruent trials in the STS and other brain regions linked to social cognition, indicating a strong effect of intention in typically developing subjects. The same brain regions were activated during observation of gaze shifts in subjects with autism (Figure Ic), but this did not differ between congruent and incongruent trials, indicating that activity in these regions was not modulated by the context of the perceived gaze shift. These results demonstrate a difference in the response of brain regions underlying eye-gaze processing in ASD.

(a) Viewing animations that elicited mentalizing

Control group   ASD group
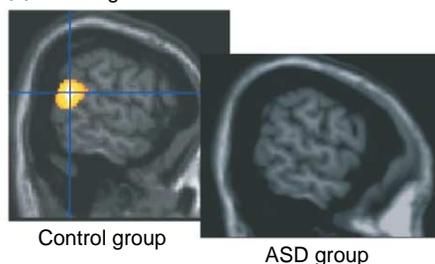
(b) Listening to human voice

Control group   Autistic group
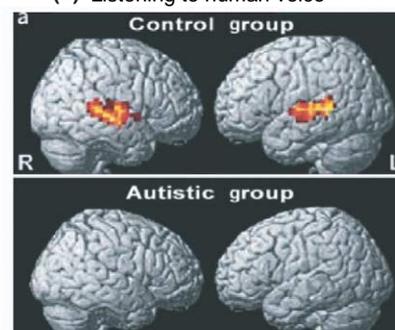
(c) Intentioned eye-gaze task

Control group   ASD group
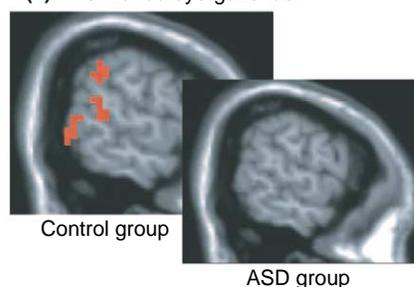
Figure I. STS and abnormal social cognition in ASD. **(a)** Abnormal activation in ASD subjects viewing animations that elicited mentalizing [13]. **(b)** Abnormal activation in ASD subjects listening to a human voice [12]. **(c)** Abnormal activation in ASD subjects during an intentional eye-gaze task [14].

are evidence that autism involves difficulty in social perception in an auditory world.

Theory-of-mind studies

Castelli *et al.* have studied cortical activation enhanced by animation of geometric figures [13]. The animations depicted two triangles moving about on a screen in three different conditions: moving randomly, moving in a goal-directed fashion (chasing or fighting) and moving interactively with implied intentions (coaxing or tricking). This third condition frequently elicited descriptions in terms of mental states that viewers attributed to the triangles (mentalizing). Ten adults with ASD and ten normal volunteers 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 normal group showed increased activation in a network previously implicated in mentalizing (involving the medial prefrontal cortex, STS and temporal poles). The ASD group showed less activation than the normal group in all these regions (Box 1). 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. However, in the autism group this region showed reduced functional connectivity with the STS (Figure 3).

More recently, Pelphrey *et al.* also found abnormal STS activation in an eye-gaze perception task in autistic adults [14]. 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 there was no difference between their activities in congruent versus 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. Pelphrey *et al.* suggested that the lack of modulation of the STS region by shifts of gaze that convey different intentions contributes to the deficits in eye-gaze processing that are associated with autism (Box 1).
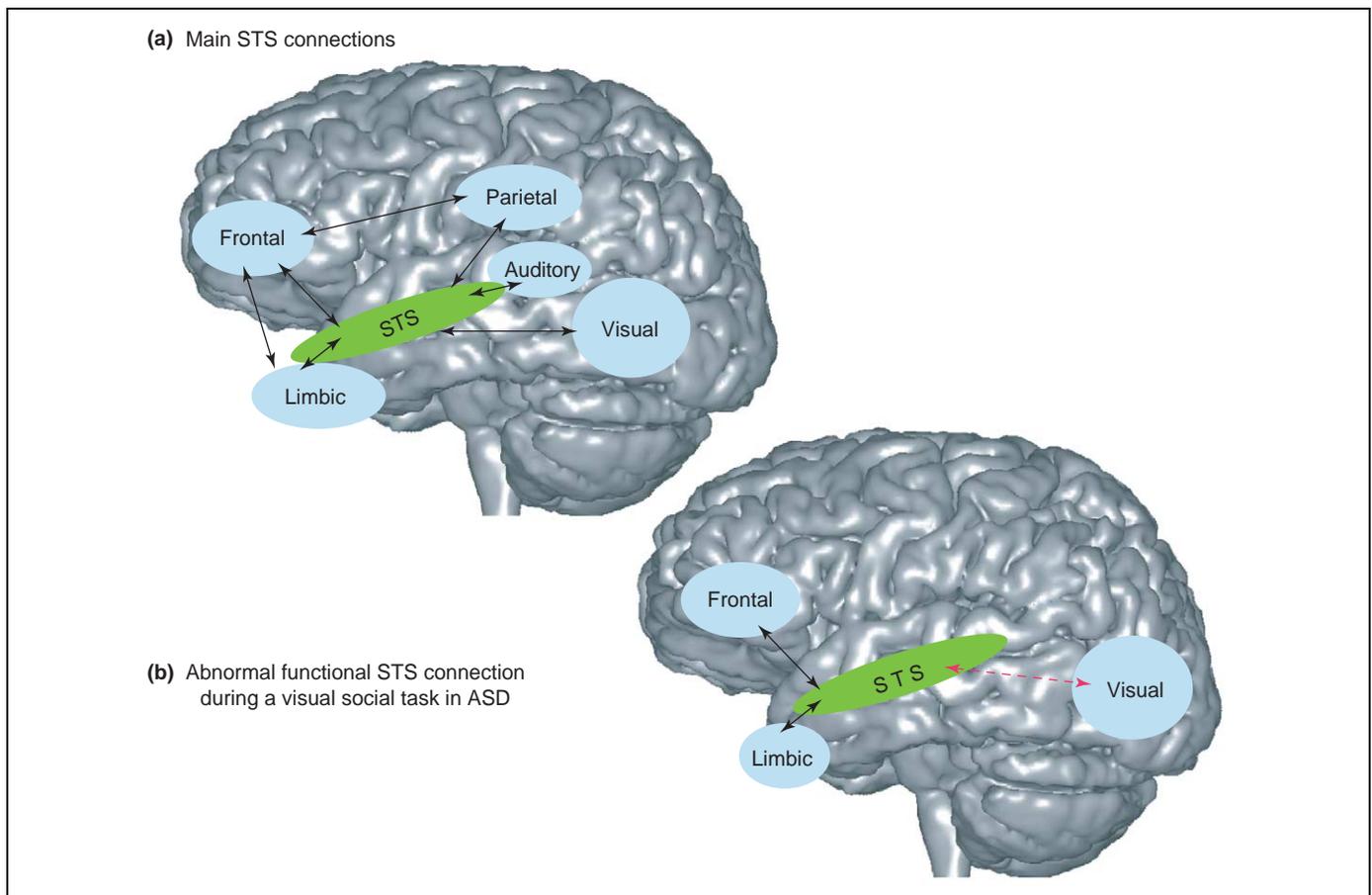
Figure 3. The STS and its connections. **(a)** The STS is a multimodal association region is strongly connected with frontal, parietal, limbic auditory and visual regions Based on anatomical studies in Refs [53,54]; adapted from Ref. [19]. **(b)** Castelli *et al.* [13] investigated the connectivity of brain regions that were activated while watching animated triangles that elicited mentalizing. They showed that, although connections to the frontal and limbic regions were normal, the visual occipital extrastriate cortex showed significantly less connectivity with the STS in ASD subjects (red broken arrow). This suggests that the difficulty experienced by the ASD group in understanding mentalizing animations might have occurred because important information about motion of the triangles was failing to be transmitted from the occipital cortex to the STS.

Concluding remarks

Several brain-imaging studies have found anatomical and functional STS abnormalities in ASD. These are characterized by decreased gray matter concentration, rest hypoperfusion and abnormal activation patterns during social cognition tasks. The STS is crucial for social cognition and is implicated in several steps of social interactions – in auditory and visual social perception (i.e. eye gazes, gestures, facial displays of emotions and voice perception) and in more complex social cognition (theory of mind and mentalizing). In addition, the STS is highly connected with other regions of the 'social brain' such as the FFA, the orbitofrontal cortex and the amygdala (Figure 3). All these regions were found to be abnormally activated in ASD during tasks implicating social cognition. Therefore, the brain-imaging data reviewed here suggest that abnormalities in the STS could be the first step in the cascade of abnormal neural phenomena underlying ASD. Early developmental neural abnormalities of the STS would lead to abnormal connectivity among key regions of the social brain in ASD. Future diffusion-tracking fiber studies and longitudinal brain-imaging studies in ASD will enable better investigation into these hypotheses. Nevertheless, these data provide a new outlook for understanding of ASD, arguing for a deficit in the perception of socially relevant stimuli. This outlook might facilitate development new therapy approaches, with a focus on the innate processing and perception of face, eye-gaze and voice stimuli.

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