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The posterior superior temporal sulcus is involved in social communication not specific for the eyes

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ABSTRACT

Neuroimaging and lesion studies suggest that the superior temporal sulcus (STS) region is involved in eye gaze processing. Hence, the STS region is suggested to be the location of the "eye-direction detector", a key element in the "mindreading model" proposed by Baron-Cohen [Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind*. Cambridge: The MIT Press]. Not only the eyes, but also a pointing finger of another person can inform us about the direction of attention of the other one. In an event-related functional magnetic resonance imaging experiment, healthy human subjects actively followed a directional cue provided either by the eyes or, alternatively, the pointing finger of another person to make an eye movement toward an object in space. Our results show clearly that the posterior STS region is equally involved in processing directional information from either source. The only difference between the two cues was found in the lingual gyrus, in which a stronger blood-oxygen-level-dependent (BOLD) response was observed during the finger pointing compared to the gaze following task. We suggest that different structures might be involved in the initial processing of directional information coming from the eyes or the pointing finger. These different streams of information may then converge in the posterior STS region, orchestrating the usage of a wider range of socially relevant directional cues able to inform us about the direction of attention and the intentions of another person.

1. Introduction

Our understanding of the direction of attention of another person is crucial for normal social interactions. It informs us about the object of interest of the other person and is a prerequisite for deriving a "theory of mind" (Emery, 2000). So far, researchers have focused almost exclusively on the directional information coming from the eyes of another person. One example is the well known "mindreading model" proposed by Baron-Cohen (Baron-Cohen, 1995, p. 32). A central module in this model is the eye-direction-detector (EDD) which is used to compute the direction of eye gaze of another person and when linked to the shared-attention mechanism (SAM) enables us to "read" the mental state of the other person. According to Baron-Cohen, one possible location of the EDD is the superior temporal sulcus (STS) (Baron-Cohen, 1995, p. 88). The first evidence for this location dates from the early 1980s when electrophysiological studies in monkeys showed that the STS contains cells that respond selectively to faces (Bruce, Desimone, & Gross, 1981; Perrett, Rolls, & Cann, 1982) and, more specifically, cells were found that respond to the direction of gaze (Perrett et al., 1985). The second line of evidence comes from a lesion study in macaques, which showed that after bilateral removal of the banks and floor of the STS, monkeys were impaired in their ability to discriminate between different angles of eye gaze (Campbell, Heywood, Cowey, Regard, & Landis, 1990). More recently, a positron emission tomography (PET) study revealed that during processing of direct and averted gaze several brain regions are specifically activated, including parts of the middle temporal gyrus (MTG) (Wicker, Michel, Henaff, & Decety, 1998). This study was followed by functional magnetic resonance imaging (fMRI) studies showing that passive viewing of shifts of eye gaze activates especially the posterior part of the STS (Hoffman & Haxby, 2000; Hooker et al., 2003; Pelphrey, Viola, & McCarthy, 2004; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Puce, Allison, Bentin, Gore, & McCarthy, 1998). The posterior MTG and the STS are both located in a region, usually referred to as the STS region, a somewhat unfortunate term as this region goes far beyond the fundus and the banks of the STS. Actually, the STS region as defined by Allison, Puce, and McCarthy (2000) involves the cortex within the STS, the adjacent cortex on the surface of the STG and MTG (near the straight segment of the STS), and the adjacent cortex on the surface of the angular gyrus (near the ascending limb of the STS). In a previous study, we showed that the posterior STS region is not only involved

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in the passive observation of shifts in eye gaze, but additionally in extracting and using detailed directional information from the eyes of another person to redirect our own gaze and establish joint attention (Materna, Dicke, & Thier, 2008). In this study, subjects had to use two different types of cues to reorient their attention to a target in space. The first cue was a socially relevant directional cue (eye gaze direction), the second cue was a non-social symbolic cue (iris grey value). During both conditions a significant blood-oxygen-level-dependent (BOLD) response was observed in areas involved in spatial attention (intraparietal sulcus), decision-making (dorsolateral prefrontal cortex), and the control of goal-directed eye movements (frontal eye field, supplementary eye field and superior colliculus). The only region showing a different response when subjects were using eye gaze direction compared to using iris grey value to reorient attention was the bilateral posterior STS region.

Eye gaze is not the only social cue guiding attention. Also head and body orientation or a pointing finger can inform us about the focus of attention of another person. One important question regarding the posterior STS region that has not been addressed as yet is whether it contains a dedicated eye gaze processor, restricted to the detection and use of directional information coming from the eyes, or whether this region houses a more general processor able to tune in on a larger spectrum of socially relevant directional cues, able to inform us about the direction of attention of another person.

In their review paper, Langton, Watt, and Bruce (2000) argued that the emphasis on eye gaze within models like the "mindreading model" (Baron-Cohen, 1995) has led to the neglect of other important directional cues from the head, the body posture or gestures such as a pointing finger. Indeed, psychophysical studies have indicated that, in addition to eye gaze cues, head orientation and pointing gestures contribute to decisions we make about the direction of another ones attention (Langton, 2000; Langton & Bruce, 2000). Another indication that not only eye gaze is important for social communication, comes from studies in people who suffer from disturbances of social cognition, like people with autism spectrum disorders. Again many studies on such disturbances have focussed on processing directional information from the eyes and found that this process is disturbed in people with autism (for reviews see Emery, 2000; Nation and Penny, 2008).

However, also the use and understanding of finger pointing in its "protodeclarative form" (pointing with the index finger to indicate interest in an object) is impaired in people with autism (Baron-Cohen, 1989; Baron-Cohen et al., 1996; Curcio, 1978; Warreyn, Roeyers, Van Wetswinkel, & De Groote, 2007). In an anatomical MRI study using whole-brain voxel-based morphometry (VBM) Boddaert et al. (2004) showed that specifically in the STS, autistic children have a significantly decreased grey matter concentration compared to healthy controls. In another anatomical MRI study Levitt et al. (2003) created a detailed map of the 22 major brain sulci in autistic and healthy children and found an anatomical shift of primarily the frontal and temporal sulci, including the STS, in autistic children. Since people with autism are impaired in the use of directional information from both the eyes and the pointing finger of another person, this again suggests a possible broader role of the STS region in the perception and use of different socially relevant cues than known so far.

An argument against the idea of a broader role of the STS region comes from two fMRI studies in which a topography for different body parts motion was found in the STS (Dubeau, Iacoboni, Koski, Markovac, & Mazziotta, 2002; Pelphrey et al., 2005). In both studies subjects passively viewed pictures of moving eyes, a moving mouth, and a moving finger/hand. Dubeau et al. found that the finger representation was located most dorsal in the STS, and the STS mouth area was located more anterior compared to the STS eyes area. Pelphrey et al. found similar locations for the eye and mouth representation, the mouth area being located anterior compared to the eye area. However, in their study the hand representation was located inferior and posterior compared to the eye area. In the latter two studies the STS eyes area was located in the posterior STS region (on the straight segment of the STS near the ascending limb of the STS). In both studies subjects passively viewed different body parts motion.

The aim of this study was to answer the question: do we also find activation in dissociable areas of the STS region when subjects are actively using directional information from different body parts to reorient their attention to an object in space? Or, alternatively, is the posterior STS region more generally involved in the analysis and use of socially relevant directional cues? In the latter case one would expect to find a similar activation of the posterior STS region when different directional cues are used.

To answer this question we performed an fMRI study in which subjects had to follow a directional cue either provided by the eyes or by the finger of another person toward an object in space and establish joint attention. In order to do so, they either had to extract the gaze direction of the eyes of a person presented on a screen (condition 1: gaze following) or, alternatively, they had to extract the direction of the pointing finger of this person (condition 2: finger pointing) in order to guide a saccade to one out of five possible targets. The saccade targets where five pins presented on the lower border of the stimulus image.

In previous studies (Dubeau et al., 2002; Pelphrey et al., 2005) different stimuli were compared that were not physically identical. The aim of our study was to reveal whether the same or different regions of the STS are involved in *using* different socially important directional cues to reorient our gaze direction. To exclude the possibility that the different physical properties of the stimuli would account for different brain activations, we compared two conditions that were physically identical.

This means that during both conditions subjects perceived both eye and finger movements. However, depending on the instruction either the directional information from the eyes or the directional information from the finger was used to redirect gaze. In other words, in contrast to previous studies we compared two conditions that were physically identical but differed cognitively.

2. Materials and methods

2.1. Subjects

Seventeen right-handed healthy volunteers (8 women; age range 20–34 years) participated in this study, which was approved by the Ethics Review Board of the Tübingen Medical School. All participants had normal or corrected-to-normal vision. Each subject provided written informed consent and was compensated for participating.

2.2. Experimental task

Each session started with an instruction screen, instructing the subjects whether they had to follow the eye gaze (condition 1) or the pointing finger (condition 2) in a picture of a person presented on the screen (see Fig. 1). After 5 s the first block started with a picture of a person whose head and eyes were oriented straight ahead, and also his finger was pointing straight ahead into the camera. Subjects had to fixate a dot positioned in between the eyes for 6–10 s (baseline). Then, on the next picture, both the position of the eyes and the finger had changed. During the gaze following blocks subjects now had to figure out to which of the five targets the person on the picture was looking and then had to make an eye movement to this target. They were instructed to ignore the directional information from the pointing finger. During the finger pointing blocks, conversely, subjects had to ignore the shift in eye gaze and had to make an eye movement to the target to which the finger was pointing. Subjects were instructed to fixate on the chosen target for 3 s until the 'baseline picture' appeared again. The gaze and finger pointing directions were randomized, meaning that in four out of five trials the directional cues were incongruent and in one out of five trails they were congruent with each other.

Every block contained 10 trials (either gaze following or finger pointing) and every session consisted of two gaze following and two finger-pointing blocks. Each