

# Superior Temporal Sulcus—It's My Area: Or Is It?

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## Abstract

■ The superior temporal sulcus (STS) is the chameleon of the human brain. Several research areas claim the STS as the host brain region for their particular behavior of interest. Some see it as one of the core structures for theory of mind. For others, it is the main region for audiovisual integration. It plays an important role in biological motion perception, but is also claimed to be essential for speech processing and processing of faces. We review the foci of activations in the STS from multiple functional magnetic resonance imaging studies, focusing on theory of mind, audiovisual integration, motion processing, speech processing, and face processing. The results indicate a differentiation of the STS region in an anterior

portion, mainly involved in speech processing, and a posterior portion recruited by cognitive demands of all these different research areas. The latter finding argues against a strict functional subdivision of the STS. In line with anatomical evidence from tracer studies, we propose that the function of the STS varies depending on the nature of network coactivations with different regions in the frontal cortex and medial-temporal lobe. This view is more in keeping with the notion that the same brain region can support different cognitive operations depending on task-dependent network connections, emphasizing the role of network connectivity analysis in neuroimaging. ■

## INTRODUCTION

In the last decade, the human superior temporal sulcus (STS) and surrounding regions have been widely studied. Paradoxically, the exploding numbers of findings have made the role of the STS region in the human brain even more mysterious. The STS is a major sulcal landmark in the temporal lobe and adjacent cortices on the surface of the superior and middle temporal gyri (STG and MTG, respectively) and the angular gyrus at the intersection to the inferior parietal lobe posteriorly. The STS is claimed to be the host brain region for theory of mind (ToM) and social perception (Saxe, 2006; Zilbovicious et al., 2006; Gallagher & Frith, 2003), but also for audiovisual (AV) integration (Amedi, von Kriegstein, van Atteveldt, Beauchamp, & Naumer, 2005; Beauchamp, 2005; Calvert, 2001). For some, it is the prime brain structure for biological motion processing (Puce & Perrett, 2003; Allison, Puce, & McCarthy, 2000), whereas others discuss it in the context of speech perception (Price, 2000) and face processing (Haxby, Hoffman, & Gobbini, 2000).

What is the secret of the multifunctionality of the STS region? One assumption is that a large structure as the STS and its adjacent cortices has some regional specialization. According to this assumption, for example, one subsection of the STS region might mainly be associated with ToM and social perception, whereas another distinct STS region might host AV integration. The results of studies on patients with lesions in the STS region are

often interpreted in line with this assumption. For example, the left STS region is seen as a prime area for speech processing (Wernicke, 1874), with the MTG being more strongly involved in word comprehension, and the anterior STG, STS, and angular gyrus being more important for sentence processing (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004). At the same time, a particular region in the upper bank of the left STS, intersecting the parietal lobe, has been proposed to be the host of ToM because patients with a lesion in this region showed a deficit in a false belief task (Samson, Apperly, Chiavarino, & Humphreys, 2004). The anterior portion of the right STG was suggested to play a role in spatial awareness because it was shown to be the center of lesion overlap in neglect patients (Karnath, 2001). Other authors claim that the right STG hosts biological motion processing because a patient with a lesion circumscribing the entire right STG showed a deficit in biological motion perception (Akiyama, Kato, Muramatsu, Saito, Nakachi, et al., 2006; Akiyama, Kato, Muramatsu, Saito, Umeda, et al., 2006). The observation of a behavioral deficit can make a strong case for the function of a particular damaged brain region. However, such conclusions have to be drawn with caution. It is fair to say that lesions exclusively focusing on the STS region are rare in humans and that most patients exhibit deficits in more than one function. For example, Akiyama et al.'s patient showed spatial neglect in the acute stage, besides the impairment in biological motion processing. Samson et al.'s patients had deficits in speech comprehension in addition to impairment in ToM. One explanation is that

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the patients' lesions extended from, for example, the "ToM region" to the "speech processing region" of the STS. Alternatively, the finding that lesions in similar STS regions cause different functional deficits could argue against a strict functional subdivision.

Lesion studies or single-cell recordings in nonhuman primates are spatially more precise than lesions in the human brain. Although the comparability of human and monkey STS is uncertain, there are similarities in anatomical projections, permitting assumptions about the human STS on the basis of nonhuman data (Keysers & Perrett, 2004; Petrides & Pandya, 2001). There are a number of findings indicating that a region in the anterior portion of the upper STS is selectively involved in the processing of body movements, including gaze direction (Oram & Perrett, 1994, 1996; reviewed in Keysers & Perrett, 2004). Other single-cell studies report neurons in the STS region, which selectively respond to moving images, faces, or nonface complex visual stimuli (Desimone & Ungerleider, 1986; Van Essen, Maunsell, & Bixby, 1981; Seltzer & Pandya, 1978). Most of these neurons are reported in a multimodal region (TPO) in the upper bank of the STS (Baylis, Rolls, & Leonard, 1987). This multimodal region could be distinguished from a more dorsal area involved in auditory processing (TAa) and a more ventral region which mainly processes visual stimuli (TEa and TEM) (Baylis et al., 1987). Apart from preferences for input modalities and visual properties, the different STS regions are also characterized by the pattern of anatomical connections with other brain regions (Seltzer & Pandya, 1989a, 1994). The auditory and multimodal sections in the upper bank of the STS (TAa and TPO) are reciprocally connected with the frontal cortex. The anterior portion of the multimodal TPO projects to and receives inputs from ventral and medial areas of the frontal lobe, which themselves project to the limbic system (Barbas, 2000; Carmichael & Price, 1995). The middle portion of the TPO is mainly connected to lateral prefrontal regions around the principal sulcus. The posterior portion of the TPO projects to dorsal prefrontal and premotor areas. Moreover, all STS subregions project to the parietal cortex. The three TPO subregions differ not only in intercortical connectivity but also in cytoarchitectural and chemoarchitectural properties. The posterior TPO is characterized by large pyramidal neurons in layer III and clearly separable layers V and VI. The middle TPO contains a well-developed layer III with medium large pyramidal cells, but no distinction between layers V and VI. The most anterior portion of the TPO is similar to the middle TPO, with even smaller pyramidal cells (Seltzer & Pandya, 1989b). In line with these cytoarchitectural properties, chemoarchitectural measures of cell density and activity (e.g., neurofilament protein [NF] immunoreactivity and cytochrome oxidase [CO] histochemistry) reveal more regular patches in the posterior TPO as compared to the medial and anterior portions (Padberg, Seltzer, & Cusick, 2003).

On the one hand, these data provide evidence for a functional subdivision of the STS region in nonhuman primates. On the other hand, the variety of reciprocal connections between certain STS regions and distinct higher-order areas could be the anatomical basis for an alternative assumption. Instead of a strict functional subdivision, the multifunctionality of the STS region might be based on coactivations with other brain regions, such as the frontal, parietal, and mesial temporal cortex. In this case, STS region activity would be determined by the nature of the network interactions with other brain regions it is coactivated with. For example, coactivation with ventral and medial frontal regions, projecting to the limbic system, might determine a role of the STS in ToM, whereas coactivation with premotor areas would make it part of the network for motion processing, and so forth. The findings from patient studies and studies on nonhuman primates, to date, are insufficient to clarify the function of the STS region in the human brain.

In this review, we consider the contribution of functional magnetic resonance imaging (fMRI) studies to this question. We review foci of activation in the STS region of multiple fMRI studies, investigating ToM, AV integration, motion processing, speech processing, and face processing. If there is regional specialization within the STS region, one would predict that foci of activations from studies investigating the same cognitive function are clustered in a particular STS subregion. A distribution of foci of activations independently of the investigated cognitive function would be more in line with the assumption that STS functions are determined via network coactivations.

## METHODS

The integration of foci of activation from multiple fMRI studies is challenging and has its own inherent problems (see also Duncan & Owen, 2000). One issue concerns statistical power. Statistical power is limited in any given study. Consequently, only a part of the activation pattern passes a certain conventional threshold. It is possible that noise differences between two studies investigating the same cognitive function might lead to activations in different subregions of the STS, even if they actually recruit a common STS subregion. The noise, which can contribute to such a pattern of results, is increased if the same cognitive function is investigated with different experimental and baseline conditions, and different stimulus material. Minimizing this source of noise requires a selection of studies which investigate the same cognitive function with comparable experimental conditions.

An equally misleading pattern of results is created if two studies, which investigate different cognitive functions, use similar experimental paradigms and overlapping stimulus material. For example, AV speech stimuli are

used to investigate speech processing (e.g., Skipper, Nusbaum, & Small, 2005) or AV integration (e.g., Calvert, Campbell, & Brammer, 2000). Even if the cognitive functions (e.g., speech processing and AV integration) recruit different STS subregions, similarities in stimulus materials alone could result in overlapping foci of activation, thus creating the illusion of a common functional correlate. To reduce erroneous clustering of activation, studies should be selected which exclusively manipulate the cognitive function in question, with the smallest possible experimental overlap with studies in other functional domains.

Finally, there may be bias introduced by the selection of the fMRI studies, which are purported to represent the individual field of research. For instance, are potential functional clusters of activity characteristics of these particular studies or representative for the field of research?

To deal with these problems, the fMRI studies included in our review were selected in three steps. In a first step, we collected fMRI studies from 1995 until April 2007 which report foci of activity in the STS and adjacent cortices (STG, MTG, and angular gyrus, including the parietal intersection) as one of their key results. To do so, we used PubMed with “superior temporal sulcus” as entry. We selected studies ( $n = 150$ ) which report results from primary analyses of human fMRI data, obtained from healthy adults. We did not include aging or exclusive child studies, or studies focused on subgroups of the healthy population, for example, subjects with synesthesia.

In a second step, based on their focus of research, the studies were grouped in five different categories of cognitive functions: ToM ( $n = 13$ ), AV integration ( $n = 14$ ), motion processing ( $n = 20$ ), speech processing ( $n = 34$ ), and face processing ( $n = 21$ ). We chose these functional categories because they were prominently linked to the STS in review papers on the individual fields of research (ToM: Saxe, 2006; Zilbovicious et al., 2006; Gallagher & Frith, 2003; AV integration: Amedi et al., 2005; Beauchamp, 2005; Calvert, 2001; biological motion processing: Puce & Perrett, 2003; Allison et al., 2000; speech perception: Price, 2000; face processing: Haxby et al., 2000). Moreover, they categorize the majority of the selected studies (102 out of 150). The remainder of the uncategorized studies focused on diverse issues such as imitation (Iacoboni et al., 2001) or different types of attention (e.g., Weissman & Woldorff, 2005; Coull, Walsh, Frith, & Nobre, 2003). It is conceivable that we might be able to establish further categories for these remaining studies, although we found it difficult because of the inhomogeneity of the designs and material employed. Accordingly, we focus on five categories to address whether the STS is organized in distinct functional subsections or more in terms of network coactivations, but cannot claim that the findings extend to all categories of cognitive processing.

In a third step, we compared studies within each functional category. The goal was to maximize the comparability and homogeneity of studies investigating the same cognitive function. We selected studies which investigated the respective cognitive function with comparable experimental and control conditions. For example, in the “Speech Processing” category, we only selected studies which presented speech-like sounds in the experimental condition and contrasted them with a non-speech control condition; for the “Motion Processing” section, we only selected studies in which motion was simulated with point-light displays, and so forth (see below). Further, we excluded studies which investigated more than one cognitive function within the same experiment. For example, in the “Speech Processing” category, we excluded studies which used emotional speech or AV speech, because in these cases neural correlates of “pure” speech processing would be modified by other cognitive functions such as emotion processing or AV integration; for the “Face Processing” category, we only chose studies with stationary faces to avoid overlap with “Motion Processing.”

The five categories are characterized in detail below, together with inclusion criteria of the studies. The studies which were chosen in this final selection step are listed in Table 1. Foci of STS activity were reported with statistical thresholds of  $p < .001$  (uncorrected) or  $q < .05$  (FDR corrected), one study reported corrected  $z$ -scores of  $>4$  (Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; see Table 1). Although statistical threshold was no selection criteria, these values indicate robust and comparable activations in the STS region in all selected studies.

### **Motion Processing**

Motion processing has been investigated in many fMRI studies with different stimulus materials such as animated figures (Thompson, Clarke, Stewart, & Puce, 2005; Pelphrey et al., 2003) or point-light displays. The latter was inspired by the ingenious work of Johansson (1973), who filmed actors dressed in black with white dots attached to their joints on a completely dark set. Based on this rudimentary information, subjects could reliably identify the walking or running motion of, for example, another person. For the “Motion Processing” section of Table 1, we only selected fMRI studies in which motion was simulated with point-light displays (Figure 1A). First, this should minimize variation in experimental and baseline conditions between the individual studies. Second, results obtained with abstract “moving dots” should reflect neural correlates of motion processing orthogonal to other categories such as face processing or ToM. Two of the selected studies reported foci from the same contrast which were separated by less than 1 cm (Noguchi, Yoshiki, Kakigi, Tanabe, & Norihiro, 2005;

**Table 1.** Paradigm, Foci of Activation, and Reference of Selected Studies

<i>Paradigm</i>	<i>Foci<sup>a</sup></i>		<i>Reference</i>
<i>Motion Processing</i>			
Point-light biological motion versus random movement	-41, -53, 12	46, -48, 12	Grossman and Blake (2002)
	-47, -42, 6	50, -33, 4*	
Point-light display walker versus "scrambled" walker; directional movement	-46, -14, -6	42, -56, 14	Vaina et al. (2001)
	-60, -12, -12	44, -68, 10	
	-46, -74, 10	( $z > 4$ )	
Point-light actions versus scrambled motion	57, -48, 12*		Peuskens, Vanrie, Verfaillie, and Orban (2005)
First-order movements (dots brighter than background), second-order movements (dots moving faster than others) versus random movement	58, -34, 4	46, 60, 10	Noguchi et al. (2005)
	46, -62, 2*		
Correlating circle movements versus noncorrelating circle movement	-60, -27, 9**		Schultz, Friston, O'Doherty, Wolpert, and Frith (2005)
<i>Speech Processing</i>			
"Sine wave speech" versus nonspeech	-61, -39, 2**		Möttönen et al. (2006)
Vowels versus nonspeech	-66, -20, 0	-60, -2, -8	Uppenkamp et al. (2006)
	66, -22, -2	48, -34, 4	
	60, -32, 2	62, 8, -18	
	58, 14, -22	44, -46, 20	
	-54, -28, -2	-64, -4, 4	
	-54, -8, 2	58, 0, -4**	
Consonants versus nonspeech; consonant-vowel syllables versus nonspeech	-59, -28, 0	-59, -27, -2	Rimol et al. (2005)
	-63, 16, -6	59, -4, 10**	
Speech versus nonspeech; average over peak coordinates from four studies	-55, -20, 0	57, -15, -2*	Binder et al. (2000)
<i>Theory of Mind</i>			
ToM stories versus non-ToM	51, -54, 27	66, -18, -15**	Saxe and Kanwisher (2003)
ToM stories and cartoons versus non-ToM	-54, -66, 22	60, -46, 22**	Gallagher et al. (2000)
Sentences (guilt, embarrassment) versus neutral	-44, -61, 20	-42, -59, 18	Takahashi et al. (2004)
	-51, -31, -7	-53, 1, -24	
	48, -7, -27*		
ToM cartoons versus non-ToM cartoons	45, -78, 18	62, 6, -5	Voellm et al. (2006)
	-59, -21, -7	-59, -57, 22*	
ToM stories and cartoons versus non-ToM	64, -49, 26	-63, -47, 23*	Kobayashi et al. (2007)
<i>Audiovisual Integration</i>			
Pictures and sounds of common objects versus fixation	-50, -55, 7**		Beauchamp et al. (2004)
Written and spoken letters versus fixation	-54, -48, 9	-46, -19, 2	Van Atteveldt et al. (2004)
	-43, -43, 23	52, -33, 18**	

**Table 1.** (continued)

<i>Paradigm</i>	<i>Foci<sup>a</sup></i>		<i>Reference</i>
White noise and checkerboards versus fixation	-51, -36, 9*		Calvert, Hansen, Iversen, and Brammer (2001)
Pictures and sounds of common objects versus fixation	-46, -76, 22*		Taylor, Moss, Stamatakis, and Tyler (2006)
Pictures and sound of common and abstract objects versus fixation	44, -43, 15	55, -29, 15**	Hein et al. (2007)
<i>Face Processing</i>			
Faces versus scrambled pictures	-45, -56, 11	50, -63, 4*	Hoffman and Haxby (2000)
Faces versus houses	-52, -61, 4	43, -57, 12*	Haxby et al. (1999)
Faces > scrambled faces	-54, -48, 4	53, -45, 7*	Ishai et al. (2005)

<sup>a</sup>The *x*, *y*, *z* coordinates according to Talairach and Tournoux (1988); Foci of activation for each study are listed in arbitrary order. They are reported with a statistical threshold of \**p* < .001 (uncorrected) or \*\**q* < 0.05 (FDR corrected).

Vaina et al., 2001). Here we included the single more significant focus.

### Speech Processing

Similar to motion processing, there is a large number of fMRI studies on speech processing. Again, our main concern was to select studies which investigated speech processing in the purest way using comparable experimental and baseline conditions. Accordingly, we only selected studies in which subjects perceived sounds with speech content versus a nonspeech baseline (Figure 1B). We did not include studies with emotional speech and experiments focusing on speech production or voice analysis (e.g., familiar vs. unfamiliar voices). The first might overlap with a different category (ToM), the latter used a variety of different experimental designs and statistical contrasts, which made it hard to compare the individual studies. In one study (Binder et al., 2000), the authors calculated the mean peak coordinate of their findings and the results of previous studies with a similar paradigm (Binder et al., 1997, 2000; Demonet et al., 1992; Zatorre, Evans, Meyer, & Gjedde, 1992). This peak coordinate is included here (see Table 1).

### Theory of Mind

Theory of mind (ToM) refers to the ability to attribute mental states to others. Typically, it is investigated with ToM stories or cartoons, describing or showing events which affect the mental state of another person in contrast to emotionally neutral non-ToM material (Figure 1C). One of the preselected studies investigated ToM in others and from the self-perspective (Vogeley et al., 2001). It was not included in the final selection because of the multifactorial design which differed from the rest of the studies

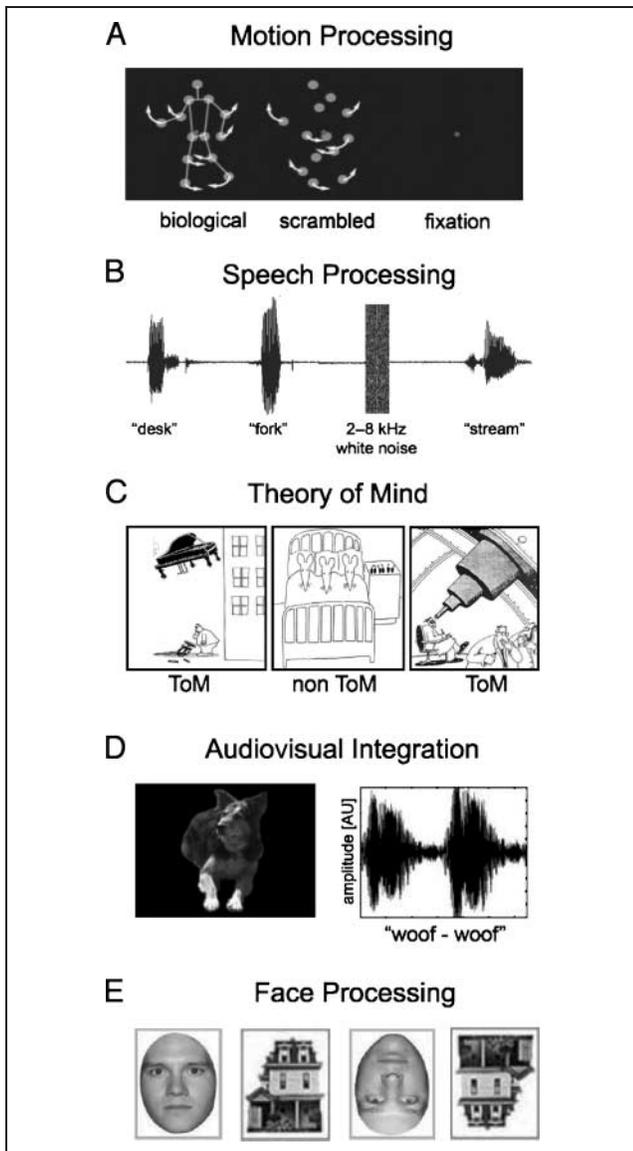
in the category. One study we included compared ToM in adults and in children (Kobayashi, Glover, & Elise, 2007). Here we used only the foci of activity reported for the ToM main effect, which is independent of the age manipulation (Table 1). One study reported the coordinate of activation overlap from ToM stories and ToM cartoons conditions (Gallagher et al., 2000).

### Audiovisual Integration

The logic of fMRI experiment on AV integration is to search for brain regions which are significantly involved in the processing of unimodal auditory and visual stimulation, but show even stronger activation if auditory and visual inputs are presented together. We selected studies that investigated AV integration with paradigms that avoided AV speech (Figure 1D; Table 1). One study was preselected, which investigated AV integration with spoken and written extracts from George Orwell's "1984" (Calvert et al., 2000). It is not part of the final selection because of the similarity in stimulation with studies of the speech processing category. The first study in the "Audiovisual Integration" section of Table 1 consisted of four experiments (Beauchamp, Lee, Argall, & Martin, 2004). The reported coordinate refers to the peak of activity in the STS region across experiments.

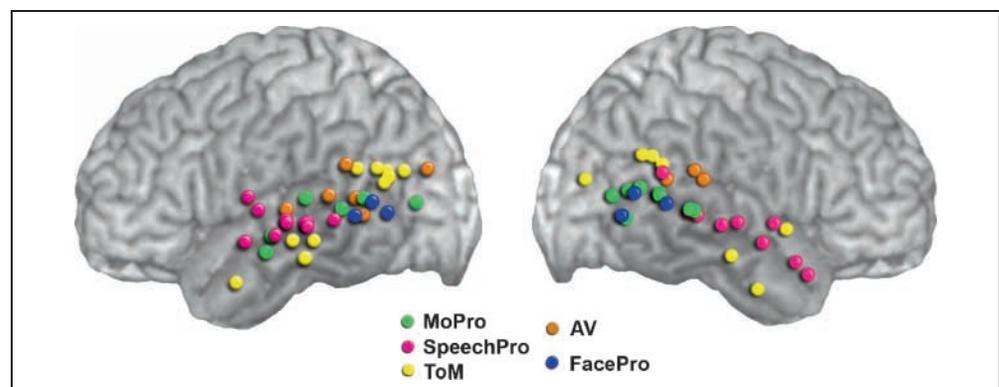
### Face Processing

The studies selected for this category investigated the neural correlates of face processing with static faces (Figure 1E). This should distinguish this category from motion processing, which is certainly involved in the processing of eye gaze and has been investigated with videos or animated stimulus material (e.g., Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005). Two of



**Figure 1.** Example stimuli for studies investigating (A) motion processing (modified from Peuskens et al., 2005, with kind permission from the *European Journal of Neuroscience* and G. Orban); (B) speech processing; (C) theory of mind (modified from Gallagher et al., 2000, with kind permission from H. L. Gallagher); (D) audiovisual integration (modified from Hein et al., 2007); (E) face processing.

**Figure 2.** Foci of activity from all selected studies rendered on a brain normalized to Talairach space. MoPro = motion processing; SpeechPro = speech processing; ToM = theory of mind; AV = audiovisual integration; FacePro = face processing.



the selected studies compared stationary faces with scrambled faces (Ishai, Schmidt, & Boesiger, 2005) or scrambled pictures (Hoffman & Haxby, 2000). One study contrasted activity elicited by stationary faces with those found for houses (Haxby et al., 1999).

## RESULTS

Combined data from all studies are shown in Figure 2. Foci of activation in the STS region have been rendered together on the surface of a brain template normalized to Talairach space. We choose Talairach space because it is commonly used in the literature and most readers are familiar with this brain mapping format. In both hemispheres, foci of activity from different cognitive functions are clustered in the posterior portion of the STS region. Activation in more anterior areas was associated to speech processing and ToM. To obtain a more objective criterion for these observations, we performed a cluster analysis using a two-step clustering algorithm. A first step of this analysis determined the number of clusters based on the Schwarz's Bayesian Criterion (BIC) and defined their centers. In a second step, variables (here the  $x, y, z$  coordinates of the individual foci of activation) were merged together based on their distances (here Euclidian distance) until the determined number of clusters was reached (Norusis, 2007; Hartigan, 1975). We chose this two-step algorithm because clusters are determined based on information theoretical criteria and, in contrast to other cluster procedures, no pretest assumptions about the number of clusters are required.

The result of the clustering algorithm determined two clusters in each hemisphere (Table 2). In more detail, clusters of activity were found in the anterior portion of the STS region in the left ( $x = -57, y = -19, z = -4$ ) and right ( $x = 59, y = -7, z = -10$ ) MTG and in the posterior portion of the STS region in the left ( $x = -49, y = -55, z = 14$ ) and right ( $x = 50, y = -49, z = 13$ ) STG (Table 3). The robustness of the results of the cluster analysis was tested with the Kolmogorov-Smirnov Test, a well-known nonparametric test for dif-

**Table 2.** Cluster Distribution

	<i>n</i>	% of Combined	% of Total
<i>Left Hemisphere</i>			
Cluster			
1	17	48.6	48.6
2	18	51.4	51.4
Combined	35	100.0	100.0
Total	35		100.0
<i>Right Hemisphere</i>			
Cluster			
1	20	66.7	66.7
2	10	33.3	33.3
Combined	30	100.0	100.0
Total	30		100.0

*n* = number of activation foci.

ferences between distributions which can be applied to three-dimensional datasets such as *x*, *y*, *z* brain coordinates (Peacock, 1983; see also Duncan & Owen, 2000). The results of this analysis confirmed that there are significant differences between the distributions of activation foci in the anterior and the posterior cluster of each hemisphere, all  $p < .01$ .

Next, we assessed which of the variables (*x*, *y*, *z* brain coordinates) were most important for the formation of the different clusters by comparing the distribution of each of the variables within each cluster to the overall distribution of values of all cases (for details, see Norusis, 2007). The results are visualized in Figure 3. The critical value line provides information of how dissimilar each cluster is from the average. If the absolute value of the statistics for a cluster is greater than the critical value, the variable is important in distinguishing that cluster from the others. Figure 3 shows that, in both hemispheres, clusters are mainly formed based on differences in the anterior to posterior (*y*-coordinate) and superior to inferior (*z*-coordinate) dimension, but are less distinct in the horizontal location of the activation foci (left–right; *x*-coordinate).

Finally, we investigated differences in the distribution of activation foci between posterior and anterior clusters for each cognitive function separately, using chi-square tests. The majority of activation foci for motion processing and AV integration, and all of the foci for face processing, were clustered bilaterally in the posterior portion of the STS region (motion processing,  $\chi^2 = 13.7, p < .001$ ; AV processing,  $\chi^2 = 5.4, p < .02$ ; Figure 4). Foci of activity for speech processing were predominately located in the left and right anterior clusters ( $\chi^2 = 47.4, p < .001$ ). ToM activations were equally distributed over all four different clusters ( $\chi^2 = 1.06, p > .3$ ).

Taken together, the results of the cluster analysis indicate functional subdivision of the STS region in two areas; an anterior region mostly associated with speech processing and, to a lesser extent, with ToM functions, and a posterior region involved in face processing, AV integration, motion processing, and ToM.

## DISCUSSION

We reviewed foci of activity in the STS region from multiple fMRI studies, which investigated diverse cognitive functions such as ToM, AV integration, motion processing, speech processing, and face processing. One hypothesis was that the multifunctionality of the STS and adjacent cortices is based on a functional subdivision, which would predict that activation foci for different cognitive functions cluster in distinct STS subregions. Another notion was that the different functions of the STS region are determined by the functional characteristics of coactivated higher-order brain regions, rather than by functional fragmentation of the STS itself. In this case, similar STS regions could subservise various cognitive functions. This would lead to the prediction that foci of activity for different cognitive functions are located in overlapping regions of the STS.

Our results revealed distinct clusters of activations in the anterior and in the posterior portions of the STS region in both hemispheres. Foci of activity for speech processing were mainly located in the anterior STS region, whereas motion processing, AV integration, and face processing recruited posterior portions. This might imply some differentiation between the anterior and posterior STS. A closer inspection of the composition of the clusters (Figure 4) reveals that even the more “specialized” anterior portion of the STS is not exclusively related to speech processing. According to these results,

**Table 3.** Cluster Profiles

Cluster	<i>x</i>		<i>y</i>		<i>z</i>	
	Mean	SD	Mean	SD	Mean	SD
<i>Centroids Left Hemisphere</i>						
Cluster						
1	−49.7	6.2	−55.4	10.8	14.3	7.3
2	−57.0	5.6	−19.0	10.9	−3.7	7.5
Combined	−53.4	6.9	−36.7	21.3	5.0	11.7
<i>Centroids Right Hemisphere</i>						
Cluster						
1	49.9	6.26	−49.3	13.1	12.8	7.4
2	59.6	5.17	−7.0	14.6	−10.3	9.7
Combined	53.1	7.46	−35.2	24.3	5.1	13.73

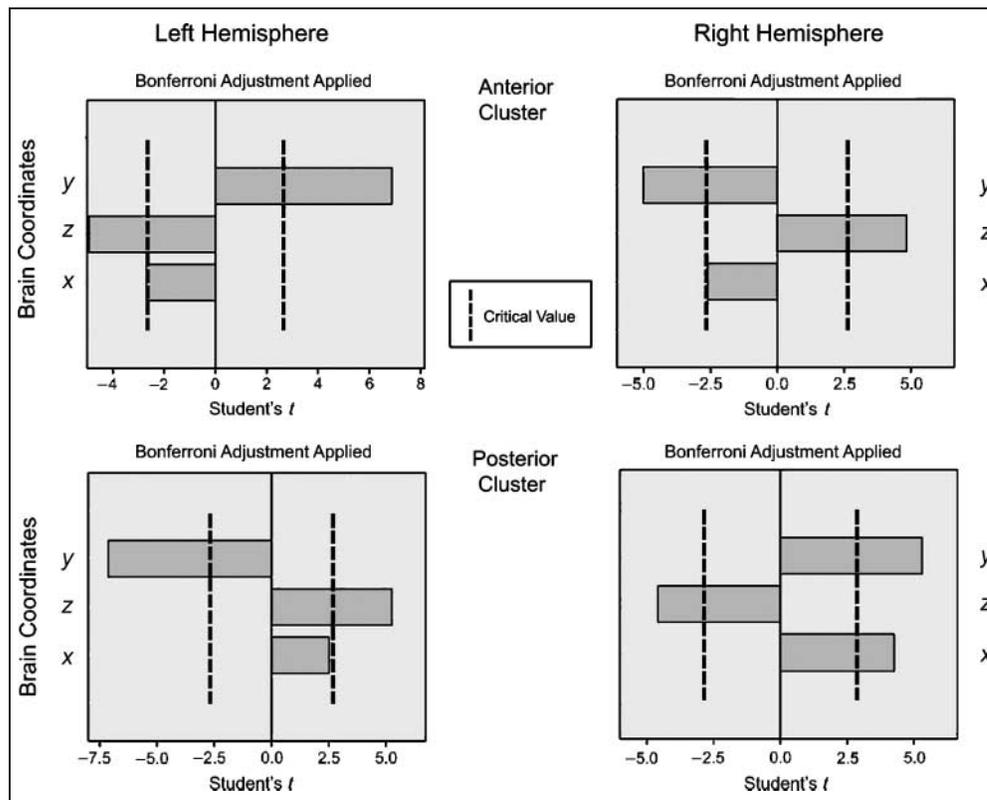
the differentiation between the anterior and posterior STS cluster might rather reflect differences in the degree of multifunctionality than a functional subdivision. Foci of activation were clustered together based on the distance between the individual brain coordinates, which indicates that different cognitive functions recruit similar STS regions. This is supported by the results of a recent fMRI study (Mitchell, 2008), which analyzed effects of a nonsocial attention tasks in regions of interest localized with ToM material (Saxe & Kanwisher, 2003). Activity in the “ToM regions” in posterior STS, intersecting the parietal lobe, also correlated with differential effects in attentional reorienting. In line with our findings, this argues against distinct functional subregions in the STS and adjacent cortices and is more in favor of the assumption that the same STS region can serve different cognitive functions, as a flexible component in networks with other brain regions. There is abundant evidence for this proposition from neuroanatomical studies revealing bidirectional connections of the STS region with a variety of brain structures, such as the ventral and medial frontal cortex, lateral prefrontal and premotor areas, the parietal cortex, and mesial temporal regions (Seltzer & Pandya, 1989a, 1994).

In line with the network assumption, four of the five studies in the “ToM” category (Kobayashi et al., 2007; Voellm et al., 2006; Takahashi et al., 2004; Gallagher et al., 2000) report medial prefrontal activity together with STS activation, whereas STS activity in speech pro-

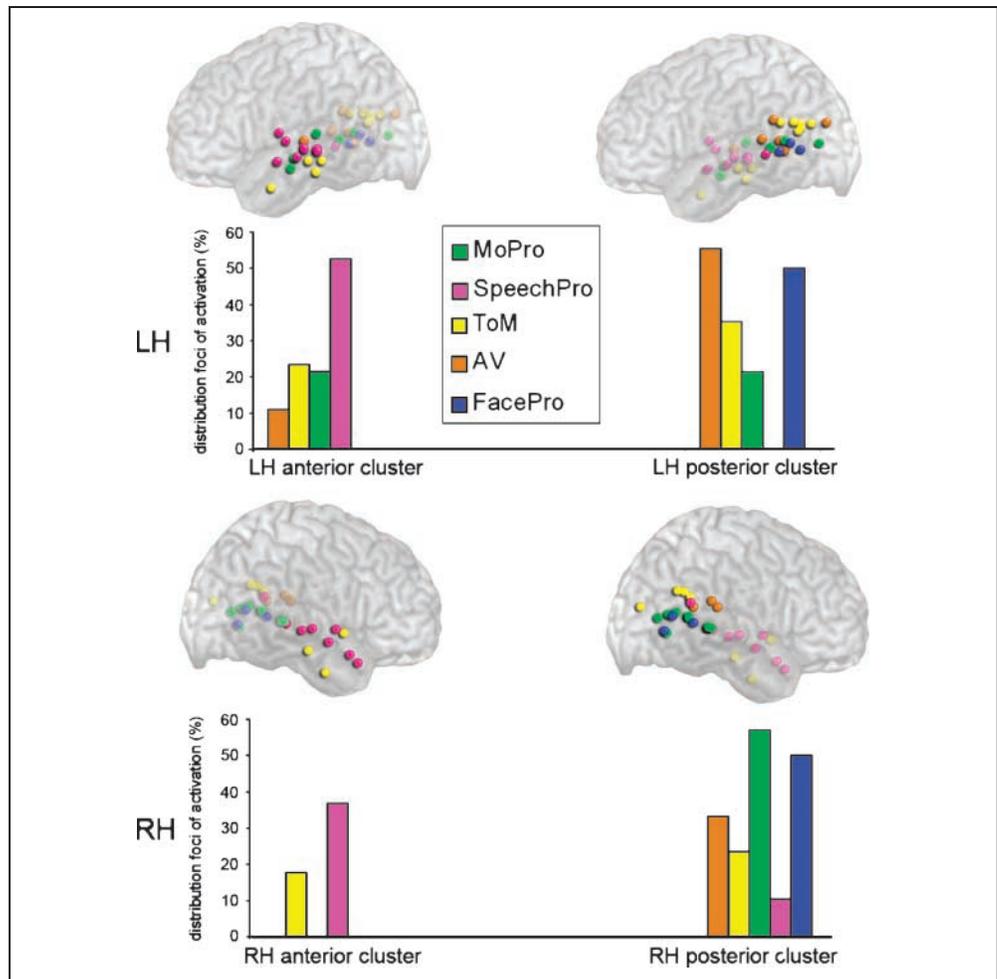
cessing was more accompanied by inferior frontal activation (Uppenkamp, Johnsrude, Norris, Marslen-Wilson, & Patterson, 2006; Rimol, Specht, Weis, Savoy, & Hugdahl, 2005). This might imply that the STS serves ToM when coactivated with medial prefrontal regions, while being involved in speech processing when coactivated with the inferior frontal cortex. It is important to note that the present dataset only provides limited information about the functional connectivity and, presumably, communication of the STS with other brain regions. First, because all the reviewed studies used conventional methods of fMRI analysis, which are suitable for the localization of neural activity, but not for the analysis of neural network function, and second, some of the selected studies focused exclusively on the STS region and did not acquire and analyze imaging data from other brain regions (e.g., Van Atteveldt, Formisano, Goebel, & Blomert, 2004; Binder et al., 2000).

An explicit testing of the network assumption is possible with more recent analysis methods, which permit analysis of activity in the STS region as part of an integrated neural network. One group of methods assumes that communication between different brain regions is reflected in covariance of changes in activity. In structural equation models (SEMs), such covariances are tested within a restricted anatomical model, which makes a priori assumptions about the causality of neural interactions (Penny, Stephan, Mechelli, & Friston, 2004; Büchel & Friston, 1997, 2000; MacIntosh & Gonzalez-Lima, 1991).

**Figure 3.** Formation of clusters based on *x*, *y* and *z* brain coordinates.



**Figure 4.** Clusters in anterior and posterior STS regions determined by the two-step clustering algorithm and distribution of foci of activation of the five different cognitive functions. LH = left hemisphere; RH = right hemisphere; MoPro = motion processing; SpeechPro = speech processing; ToM = theory of mind; AV = audiovisual integration; FacePro = face processing.



For example, based on the anatomical connections shown in nonhuman primates, STS activity might covary with premotor activity, determining a function of the STS region in motion processing, whereas covariance with medial frontal activity might determine a function in ToM. Similar to SEM, dynamic causal models (DCMs) are also based on changes of neural activity in different brain regions, but explore such changes as a function of external input and not within a restricted anatomical model (Friston, Harrison, & Penny, 2003).

More recent approaches incorporated the notion that efficient communication between different brain regions requires changes in activity, which are coherent in time (Fries, 2005). One group of methods is based on principles of coherence analysis and interfrequency coupling, applied to a range of oscillatory signals recorded from human electroencephalography or magnetoencephalography, and animal single-cell data or local field potentials. Moreover, this approach has been successfully implemented in the analysis of low-frequency signals in fMRI data (Curtis, Sun, Miller, & D'Esposito, 2005; Sun, Miller, & D'Esposito, 2004, 2005). Another novel approach uses a measurement from information theory (mutual information) to determine the information shared

by different brain regions at a given time, which is then used to specify the temporal characteristics of information flow between different brain regions (Fuhrmann Alpert, Sun, Handwerker, D'Esposito, & Knight, 2007; Fuhrmann Alpert, Hein, Tsai, Naumer, & Knight, in press). The assumption would be that the coherence in activity and the information flow between the STS region and higher-order brain regions varies as a function of the investigated cognitive function.

There are only few studies that have investigated STS coactivations in the human brain with these methods. Two recent studies applied DCM and showed strong connections between the STS and early auditory regions (Noppeney, Josephs, Hocking, Price, & Friston, 2007; Sukhbinder, Stephan, Warren, Friston, & Griffiths, 2007). Another study used SEM to explore the connectivity of the STS, the early auditory cortex, and the frontal cortex when subjects listen to human footsteps (Caclin & Fonlupt, 2006). Their results revealed a network of early auditory regions, the STS and the parietal lobe, which were modulated by the dorsolateral prefrontal cortex. This is in line with the assumption that top-down signals between different brain regions regulate the flow of information in distributed neural networks, strongly

supported by recent single-cell results (Buschman & Miller, 2007; Saalman, Pigarev, & Vidyasagar, 2007; Womelsdorf et al., 2007; reviewed in Knight, 2007). The findings of Buschman and Miller (2007) indicate that the interaction between brain regions, in their case, the monkey prefrontal and the parietal cortex, changes flexibly with changes in cognitive task demands. Along the same lines, intracranial data from subdural electrodes in the human cortex have shown that interfrequency coupling of oscillation in different brain regions correlates to different cognitive functions (Canolty et al., 2006).

Taking this work and our cluster analysis into consideration, we propose that the multifunctionality of the STS region is determined by flexible network coactivations with other brain regions, for example, in the frontal and medial-temporal cortex. The results of our review imply that the definition of the network interaction between the STS region and higher-order brain structures may be the key to understanding cognitive functions such as ToM, AV integration, motion processing, speech processing, and face processing, and emphasize the role of implementing network connectivity analysis in neuroimaging.

## Acknowledgments

We thank Clay Clayworth for help with preparing the figures and Vincent van Veen for helpful comments on data analysis and the manuscript. This work was supported by the German Research Foundation (HE 4566/1-1; G. H.) and NINDS grants NS21135 and PO40813.

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