

The social mysteries of the superior temporal sulcus

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The superior temporal sulcus (STS) is implicated in a variety of social processes, ranging from language perception to simulating the mental processes of others (theory of mind). In a new study, Deen and colleagues use functional magnetic resonance imaging (fMRI) to show a regular anterior–posterior organization in the STS for different social tasks.

In the human brain, the STS is second in size only to the central sulcus. Although the basic organization of the central sulcus has long been known, there is no generally accepted scheme for the organization of the STS. The fMRI study by Deen and colleagues [1] represents a step forward in understanding this fascinating chunk of the brain.

The first cognitive function ascribed to the STS was language comprehension. What we now term ‘Wernicke’s area’ comprises a posterior section of the superior temporal gyrus and middle temporal gyrus, and, by extension, the cortex between them in the posterior STS. The explosion of blood oxygen level-dependent (BOLD) fMRI studies has linked many other cognitive functions, especially those related to social cognition and perception, to the STS. To search for functional specialization within the STS, Deen and colleagues used a traditional block-design fMRI approach. The response to different conditions relative to fixation baseline was measured and the responses in selected conditions were compared to create contrasts. For the theory of mind contrast, the response to stories about beliefs was compared with the response to stories about physical properties. For biological motion, point-light displays of humans versus geometric shapes; for faces, moving faces versus objects; for voices, voice versus environmental sounds; and for language, stories versus nonsense speech.

Figure 1 summarizes two different analyses in the paper. The first analysis examined only the peak response for the different contrasts. The most posterior peak was for the theory of mind contrast, where the STS ascends sharply upwards into the inferior parietal lobule and terminates in the temporoparietal junction (TPJ). Peak responses to biological motion were more inferior where the STS begins its ascent. Peak responses to moving faces, voices, and language were progressively more anterior along the sulcus, with language peaking almost 60 mm anterior to the theory of mind peak.

The stimuli used in the study were largely taken from previously published fMRI experiments. Therefore, it is no

surprise that the activation peaks reported are similar to those found in previous experiments. For instance, the TPJ activity for theory of mind in the Deen study was within 6 mm of that previously reported [2]. This means that the posterior–anterior organization of peak coordinates can be compared with those from a meta-analysis of fMRI papers reporting STS activation [3]. Reassuringly, the results of the two approaches are in good agreement. For instance, both report both posterior and anterior theory-of-mind foci, with an intervening middle STS region responsive to biological motion.

A second analysis conducted by Deen *et al.* could not have been generated with a peak coordinate meta-analysis, because it examined the entire STS activation for each contrast instead of a single peak coordinate. The spatial extent of the STS activation map for each contrast was calculated, followed by the overlap across contrasts (a methodological note is that this analysis was properly performed within individual subjects: using group average data grossly overestimates the degree of overlap, as demonstrated by recent studies that found overlapping auditory, visual, and somatosensory responses in the STS, but not nearby areas, only with individual subject analysis [4,5]). The extent and overlap variables are related, because if two contrasts both activate a large fraction of the STS, by necessity they will have a high overlap. Indeed, overlap was observed between the language and theory of mind contrasts, two contrasts that in the left hemisphere activated most of the length of the STS. Strong overlap was also observed between moving faces and voices, contrasts that both activated a region of the mid-posterior STS.

A few cautions are in order. First, the authors examine only the STS, masking out all other brain areas even though whole-brain fMRI data were collected. This is problematic because the STS is densely connected with both early sensory cortex and association areas. Since it is certain that many of these other areas were also active, understanding the pattern of overlap across contrasts for the whole brain would provide valuable extra information. Second, the approach of Deen *et al.* reduces complex cognitive functions, such as ‘language’ to single A versus B contrasts. Although the authors used different contrasts to localize different social cognitive functions, it is not clear whether even a large number of contrasts would fully elucidate the organization of the STS in the absence of both theoretical models of the cognitive processes isolated in each contrast and neurobiological models of the neural computations underlying each process.

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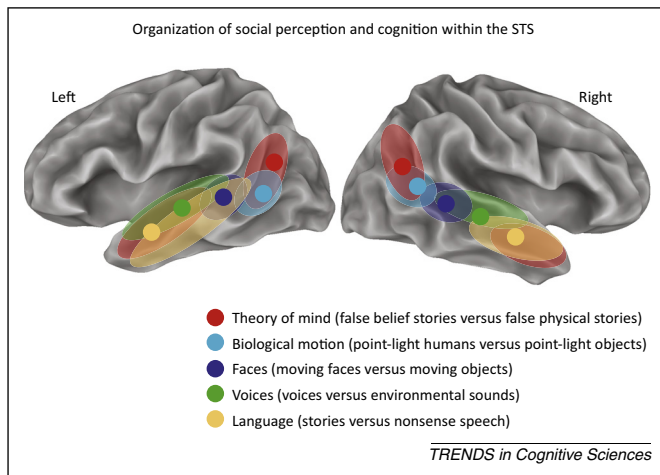


Figure 1. Organization of social perception and cognition within the superior temporal sulcus (STS). Results of Deen *et al.* [1] shown on an inflated cortical surface model of the left and right hemisphere of the N27 atlas brain. Filled circles show the location of the peak activation, averaged across subjects, for each contrast. Colored regions show the extent of the activation for each contrast (multiple colored regions for some contrasts). Based on information and data in [1].

One conceptual framework that may help guide future progress is provided by the field of multisensory integration. The authors take note that a visual contrast (faces versus objects) and an auditory contrast (voice versus environmental sounds) both activated an overlapping focus in the mid-posterior STS. However, when we speak face to face, we use both visual information from the talker's face and auditory information from the talker's voice. A theoretical model that supposes that specific visual mouth movements become linked with specific auditory speech features during language learning predicts that neurons sensitive to both complex auditory and visual features should be important for face-to-face speech perception. Correspondingly, the STS of human and nonhuman primates share an organization in which small regions of cortex that respond to unisensory visual and auditory stimuli, including faces and vocalization, are juxtaposed with regions that respond to audiovisual stimuli [6,7]. Evidence for a link between this anatomical organization and

language processing is provided by studies showing that activity in multisensory STS is correlated with behavioral measures of multisensory speech perception in adults [8] and children [9], and disrupting the STS with transcranial magnetic stimulation interferes with multisensory speech perception [10]. More generally, many forms of social communication, both verbal and nonverbal, are multisensory: a friendly pat on the back, a warm smile, or a murmur of encouragement. One attractive possibility is that, over the course of evolution and development, the multisensory anatomy of the STS has been recruited for social processes, such as theory of mind, that make use of information from multiple modalities.

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