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FEATURE ARTICLE

*On the Role of the Anterior Superior Temporal Lobe in Language Processing:
Hints from Functional Neuroimaging Studies*

Jenny Staab

Joint Doctoral Program in Language and Communicative Disorders
University of California, San Diego & San Diego State University

EDITOR'S NOTE

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On the Role of the Anterior Superior Temporal Lobe in Language Processing: Hints from Functional Neuroimaging Studies

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Abstract

A number of functional neuroimaging studies have reported activation in the left anterior superior temporal lobe (aSTL), encompassing the cortex of the anterior superior temporal gyrus and sulcus, in response to various linguistic stimuli. In this paper, I review these studies in order to explore the possible contribution of the aSTL to language processing. A specialization of the aSTL for sentence processing is unlikely, as activation in this area is not only elicited by sentences, but also by words, syllables, and even nonlinguistic auditory stimuli. It seems, however, that the aSTL responds more strongly to sentences than to other speech stimuli, and that the anterior superior temporal sulcus in particular is more responsive to speech than to other types of sound. As an alternative to a language-specific account, I suggest that the aSTL can be regarded as sensory association cortex that underlies the analysis of complex acoustic features, especially those that are typical for speech. The efficient completion of this sensory analysis is particularly critical when stimulus complexity and processing demands increase. Consequently, the amount of aSTL activation grows, as more difficult tasks have to be performed on auditory or linguistic stimuli.

Introduction

It is commonly accepted that the perisylvian areas of the dominant (left) cerebral hemisphere play an important role in the use of language and that lesions to these brain regions can engender aphasic symptoms. Traditional models of aphasia and language organization in the brain have especially focused on Broca's area in the pars opercularis and triangularis of the left inferior frontal gyrus (IFG) and Wernicke's area in the posterior part of the left superior temporal gyrus (STG). According to the well-known Wernicke-Geschwind model (e.g., Geschwind, 1972), Wernicke's area houses auditory word representations, and damage to this area would cause deficits understanding, repeating, and producing spoken and written language. Broca's area

is considered to be containing the set of articulatory forms, so that its lesion would disrupt the articulation of language.

In more recent years, it has become clear, however, that damage to these classic language zones is not the only cause of language disturbances. Moreover, a simple distinction between comprehension and articulation might not be sufficient to account for the range of aphasic syndromes. Proposals motivated by linguistic theory suggested a distinction between semantics and syntax, impairments of which would be associated with lesions in Wernicke's and Broca's area, respectively (Zurif & Caramazza, 1976). Grodzinsky (2000), for example, put forward that Broca's area is necessary for carrying out grammatical operations, and that agrammatic

comprehension and production are direct consequences of damage to the left IFG.

In contradiction to this hypothesis, Dronkers, Wilkins, van Valin, Redfern, and Jaeger (1996) showed that lesions to Broca's area are not sufficient to cause deficits in the comprehension of syntactically complex sentences. By means of cluster analysis on data from fifteen measures of morphosyntactic comprehension, they identified a group of patients with a particularly strong comprehension deficit. Although all these patients had lesions in the left IFG, there were also patients with such lesions who performed well on the comprehension task. The area that was damaged in all patients with low comprehension scores, but spared in those patients with good comprehension was a brain region outside the classic language zones, namely the anterior part of the left STG. Dronkers et al. (1996) argued that this area underlies the comprehension of complex morphosyntax.

Despite these findings, relatively little is known about the role the anterior superior temporal lobe (aSTL) plays in language processing, and the results of lesions in this area. One reason is that there are no reports of lesions that are restricted to the aSTL. Because of the blood supply pattern of the perisylvian region, strokes involving the aSTL usually affect frontal and/or more posterior temporal areas, as well. Degenerative diseases in the temporal lobes are not only diffuse in nature, but they also tend to originate in medial temporal structures before they reach superior temporal areas. Finally, lesions resulting from lobectomy are often restricted to anterior parts of the temporal lobes, yet they include inferior and medial parts, too. As medial temporal regions, namely the hippocampus, are known to be instrumental for memory, verbal memory impairments following left anterior lobectomy (Ivnik, Sharbrough, & Laws, 1987) or neural degeneration in the temporal lobe (Edwards-Lee et al., 1997) may be caused by damage to medial temporal regions, but not necessarily to the aSTL.

Similarly, studies using electrical stimulation of anterior temporal cortex have not provided clear evidence for a particular function of this region in language processing. Fedio and van Buren (1974) stimulated the superior, middle, and inferior gyri of the left temporal lobe, while subjects named pictures presented before and during the stimulation. While stimulation of anterior temporal cortex did not significantly affect immediate naming, it interfered with the naming of a picture presented before the trial on which the stimulation occurred. The authors

proposed that the anterior temporal lobe was involved in verbal storage mechanisms. A more recent study (Hamberger, Goodman, Perrine, & Tammy, 2001) also failed to find impairments in immediate picture naming as a result from anterior temporal stimulation. Naming to auditory descriptions, however, was interrupted when the subjects' anterior temporal lobe was simultaneously stimulated. As the latter task comprises both comprehension and production, it is not clear from these results which function the anterior temporal lobe might underlie. Furthermore, while both studies differentiated anterior and posterior portions, no distinction was made between superior, middle, and inferior regions within the temporal lobe. Definite statements about the aSTL can therefore not be made on the basis of these data.

A number of functional neuroimaging studies, however, have attempted to clarify the specific functional significance of the aSTL in language. These studies have employed either positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) in order to measure regional changes in cerebral blood flow (PET) or oxygenation (fMRI) while subjects processed language stimuli. Based on the association between aSTL activation and the processing of words and sentences that were observed in these studies, several authors have suggested that the aSTL is specialized for the perception of language. Yet, there is little agreement regarding the particular kind of linguistic information to which the aSTL may be sensitive, with the proposed critical properties ranging from syntactic or prosodic content (e.g., Humphries, Willard, Buchsbaum, & Hickok, 2001) to intelligibility (Scott, Blank, Rosen, & Wise, 2001) to phonological properties (Giraud & Price, 2001). Furthermore, language-specific accounts of aSTL function stand in contrast to explanations of aSTL function in terms of more general auditory processes. Binder et al. (2000), for example, argue that the aSTL, along with the rest of the human superior temporal lobe, is part of sensory association cortex involved in the analysis of complex auditory signals. In this view, the aSTL carries out higher order sensory operations that are recruited for the processing of language, without being specific to this domain.

In the remainder of this paper, I will provide an overview of neuroimaging studies reporting left aSTL activation in language tasks and the authors' interpretations of their results. In particular, I will try to assess claims that this area is specialized for particular linguistic input, which are based on the

finding of aSTL involvement in sentence, word, and syllable processing. Considering that the aSTL is also activated by the perception of complex auditory stimuli without lexical meaning or phonetic content, I will propose that one may think of it as higher order sensory association cortex instead of an area that is engaged specifically in language comprehension. Rather than being exclusively dedicated to linguistic material, the anterior STG (aSTG) seems to be carrying out the acoustic feature analyses that underlie language comprehension, and it is increasingly engaged when the comprehension task becomes more difficult. As for the left anterior STS (aSTS), experimental findings suggest that it has a stronger preference for speech sounds, as it consistently responds more strongly to speech than to pure tones, environmental sounds, as well as non-speech vocalizations. Areas of the aSTL are increasingly engaged, as sounds become more complex and the comprehension tasks more demanding.

aSTL Activation in Sentence Processing

One of the first studies to report aSTL involvement in sentence processing was conducted by Mazoyer and associates (1993). They used PET to measure regional cerebral blood flow (rCBF) changes in monolingual native speakers of French who listened to stories in Tamil as well as French word lists, jabberwocky (sentences containing phonologically legal non-words with grammatical morphemes and function words), semantically anomalous sentences, and normal discourse in French. Bilateral aSTG and temporal poles were activated in the three conditions in which speech with normal French prosody and syntax was presented. Furthermore, this activation increased with the degree of semantic coherence, with understanding the French story engendering stronger activation than the semantically anomalous sentences, which in turn elicited more rCBF change than listening to semantically void jabberwocky. The authors suggested that the temporal activation might be due to syntactic or prosodic processes or forms of verbal or nonverbal memory, as it was not present in the Tamil story or the French word list, i.e., when there was no intelligible syntactic or prosodic information.

Since Mazoyer et al. (1993) used only linguistic stimuli, aims about a language-specific role for the aSTL can easily be undermined by alternative explanations. One possibility would be that the aSTL subserves the integration or combination of potentially meaningful auditory stimuli, which do not

have to be linguistic. Humphries et al. (2001) contrasted the hypothesis that the aSTL is specialized for sentence comprehension with the alternative possibility that the anterior temporal cortex might serve the more general purpose of establishing semantic coherence by integrating stimuli over time. In order to address the issue, they conducted an fMRI experiment, in which subjects listened to sentences describing particular events or to sequences of environmental sounds describing the same events. While the sound sequences engendered measurable activity only in the middle and posterior part of the temporal lobe, listening to sentences resulted in additional activity in both aSTG and middle temporal gyrus (MTG). This difference was statistically reliable in a direct contrast of sound and sentence condition. Consequently, the authors concluded that the aSTL was involved in “sentence-level comprehension”, which should not be determined by the meaningfulness of the stimuli, since anterior temporal activation had previously been observed in response to jabberwocky (Friederici, Meyer, & von Cramon, 2000), while the meaningful sound sequences did not elicit this kind of activation.

In fact, Friederici et al. (2000) had proposed that the planum polare in the aSTG should underlie syntactic or possibly prosodic processes, independently of semantic content. In a two-factorial design, subjects were presented with normal and jabberwocky sentences, both containing syntactic information, as well as lists or real words or pseudowords without syntactic content. In contrast to the normal sentences and words, jabberwocky sentences and pseudowords did not contain semantic information. The fMRI-measured activation of the aSTG was significantly stronger for the sentences, but semantics neither produced a main effect, nor interacted with syntax; the authors took this result as evidence for the hypothesis that the aSTG subserves syntactic computations.

Another fMRI study by the same group (Meyer, Friederici, & von Cramon, 2000), demonstrated that the amount of aSTG activation depends on the grammaticality of the sentence stimuli. In this experiment, subjects listened to normal and ungrammatical sentences, and their task was either to judge the grammaticality of the sentences, or to mentally repair sentences that were erroneous. The results showed two main effects: aSTG activation was stronger for ungrammatical than for grammatical sentences, and the repair task engendered more activation than the judgment task. These activation increases were taken as an index of the additional grammatical operations that the aSTG had to carry

out when sentences were ungrammatical and especially when they had to be repaired.

In a third paper (Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002), the proposed function of the aSTL was expanded to incorporate lexical along with grammatical operations. The study compared fMRI responses to normal speech, jabberwocky, and so-called prosodic speech (speech that is filtered so that only the fundamental frequency contour and the overall amplitude envelope is preserved, while no phonetic content is present). The subjects' task was to judge whether the sentences were in active or passive mode. aSTL activation was strongest for jabberwocky, medium for normal speech, and weakest for prosodic speech. Meyer et al. (2002) argued that the stronger signal for normal speech and jabberwocky was due to the presence of syntactic information processed in the aSTL. The difference between normal speech and jabberwocky was attributed to the failed attempt to retrieve lexical information in the jabberwocky condition, resulting in stronger aSTL activation.

The problem with this interpretation is that the conditions differed not only along lexical and syntactic dimensions, but also in task difficulty as well as acoustic complexity, as the prosodic speech did not contain higher frequencies. The weak activation in the prosodic condition might simply be due to the reduced acoustic content as well as the impossibility to understand the sentences, possibly resulting in an abandon of the task (which is reflected in the subjects' at chance performance in this condition). Likewise, the stronger activation in the jabberwocky condition can be ascribed to higher task demands, as the extraction of grammatical morphemes from otherwise meaningless material may be more difficult. A similar argument can be applied to other studies reporting aSTL involvement in syntactic processing. It is, for example, plausible that processing ungrammatical sentences is more difficult and that the requirement to repair incorrect sentences makes subjects focus additional attention on the task. This can explain the activation differences found by Meyer et al. (2000), as both task difficulty and the amount of attention allocated to a task can increase the fMRI signal in sensory cortices (Büchel et al., 1998; Sanaert, van Hecke, Marchal, & Orban, 2000). As for the Humphries et al. (2001) study, the tasks of integrating words into a sentence is likely to be different from extracting meaning from a series of environmental sounds, as the sounds do not have phonological properties and they do not fulfill particular functions in the sequence as words do in a sentence.

In addition, their stimuli differed in acoustic content, and the aSTG has been shown to be sensitive to such acoustic differences (Benson et al., 2001).

Although the STG has mostly been implicated in auditory perception, Stowe and colleagues (1998, 1999) found PET activation in a study, in which visual sentences were presented. This does not necessarily contradict the assumption that the primary aSTL function is auditory, if one assumes that reading is at least partly mediated by access to the phonological code of words (Van Orden, 1991). Yet, the study provided evidence for the importance of aSTL in sentence processing, as both studies found activation in a left anterior region between STG and MTG activation in response to visually presented sentences, but not word lists. The authors attributed a language specific role to the anterior temporal cortex, yet they did not propose a specific syntactic function, but suggested that it might support a form of verbal working memory (Stowe et al., 1999). This interpretation is somewhat problematic, as no correlation between processing demands and anterior temporal activation was found: simple, complex, and ambiguous sentences elicited similar amounts of activation (Stowe et al., 1998). A possible reason for this might be the absence of an explicit task without which the subject might not have engaged additional processing resources to ensure the understanding of the sentences.

Vandenberghe, Nobre, and Price (2002) detected activity in the aSTS when they compared the PET responses to visually presented sentences and to their scrambled version, i.e. lists of words. They did not elaborate on this particular finding, as they focused on the inferior temporal pole, which was sensitive to the same distinction. Their results, however, agree with previous findings by Stowe et al. (1998, 1999).

Two further studies found the aSTL to be active during sentence comprehension. Rumsey et al. (1994) had their subjects listen to sentence pairs and judge whether these sentences had the same meaning; one of the activated regions was the anterior and middle part of the superior temporal region. Similarly, Müller et al. (1997) found left anterior portions of the MTG and STG activated when subjects listened to sentences. No inferences about the possible functional role of the aSTL in sentence processing could be made from these results, as neither study compared sentence comprehension with any other language or sound processing task.

Comparing sentence processing to the perception of other linguistic or auditory stimuli is particularly important as there are imaging studies that have

observed activation in the anterior STG, STS, or MTG in tasks that did not involve the processing of sentence- or discourse-level information. Wong et al. (2002), for example, found in their PET study that the processing of sentences as well as single words activated the aSTG, although the activation associated with sentences extended further into anterior parts. Thus, while the majority of studies suggest that aSTL regions respond more strongly to sentences than to other material, selectivity for sentence processing seems to be rather dubious.

ASTL Activation in Speech Processing

ASTL activation has been found in several studies in which subjects processed speech stimuli that did not constitute whole sentences (e.g., Binder et al., 1997). Consequently, the claim that the aSTL is uniquely devoted for sentence processing cannot be maintained. A number of studies have attempted to test the alternative hypothesis that the aSTL is involved in speech processing in general. They aimed at identifying the properties or types of information to which the aSTL is sensitive by comparing brain responses to speech with that to altered speech or different auditory stimuli.

Binder and colleagues (1997) used fMRI and had subjects either listen to tones and decide whether they were low or high in pitch, or perform a semantic decision on auditorily presented nouns. While the bilateral STG were activated in both conditions, the left STS and MTG, including their anterior part, showed activation only in the conditions involving words. The authors attributed these differences to the fact that the words, but not the tones were meaningful. They suggested that the bilateral STG might be involved in the processing of various kinds of complex sounds, while more ventral areas, including their anterior portions, should show higher order, multimodal characteristics and mediate the access to linguistic-semantic information.

In a later study, Binder et al. (2000) rejected the idea that lexical or semantic factors were critical for middle and aSTS activation. Subjects in this study listened to pure tones at different frequencies as well as to words, pseudowords, and temporally reversed words. All these conditions elicited activation in the middle part of the bilateral STG and STS, when compared to a noise baseline. Similarly to the Binder et al. (1997) study, more ventral and anterior parts were additionally recruited in the three word conditions. Since the response to words, which carry lexical-semantic information, did not significantly

differ from that to pseudowords and reversed speech, Binder et al. argued that the ventral STG and the STS were involved in the analysis of the complex acoustic features of speech.

Démonet and colleagues (1992), too, used words and pseudowords, and found aSTG activation when these conditions were compared to pitch judgment on pure tones. Yet, they did not report any aSTS activation. Equally, Giraud and Price (2001) did not find significant aSTS activation when their subjects listened to words, syllables, or environmental sounds, although the mid STS responded to all three conditions. The left aSTG was activated by speech stimuli only, and the contrast between speech and sound combined with noise was significant. From this result, the authors concluded that the aSTG is specialized for the processing of phonological input.

Sensitivity to speech sounds in the aSTL was also reported by Mummery, Ashburner, Scott, and Wise (1999). In this PET study, subjects were presented with bisyllabic nouns or with signal-correlated noise (SCN; a non-speech stimulus with the same amplitude envelope as the speech signal, but a spectrum of white noise, and thus without intelligible phonetic content). In addition, the rate of presentation was varied between 1 and 75 stimuli per minute. When comparing speech to SCN, activation was found in the bilateral STG/STS. Activation in the anterior part of this area correlated positively with the rate of presentation for speech, but not for SCN, while the posterior part was sensitive to the rate of presentation of both stimuli types. Generally, the brain area activated by speech was larger than that activated by SCN, extending more anteriorly and posteriorly. Based on electrophysiological data of superior temporal cortex function in primates, Mummery et al. proposed that the lateral STG contain unimodal auditory cortex without a specialization for speech or language, while the ventral STG and the STS receive more multimodal input and are more likely to support language functions. More specifically, they suggested that the aSTS carries out automatic prelexical processes, by which they mean the analysis of acoustic speech cues. A particular sensitivity of all parts of the left STS to speech was supported by Wise and colleagues' results, showing that PET activation in the entire anterior, middle, and posterior STS correlated with the presentation rate of speech but not that of SCN (Wise et al., 2001). As the paper focused on the posterior STG/STS, these authors did not comment on the possible function of anterior temporal cortex.

Like Mummery et al. (1999), Scott et al. (2000) found different activation patterns in the aSTG and aSTS. Their subjects listened to normal speech, rotated, noise-vocoded, as well as rotated and noise-vocoded speech. In rotated speech, the frequency spectrum is inverted; the resulting sound still resembles human phonetics, yet its formant patterns are unintelligible. Noise-vocoded speech consists of noise bands instead of voiced formants; it is comprehensible after some adjustment. When both rotation and noise-vocoding are applied, the result is unintelligible noise. Several planned contrasts were performed on the PET data. The comparison of the rotated plus noise-vocoded speech with the other three conditions was meant to reveal activation that was specific to phonetic input, and a significant effect was found in the left STG and the posterior STS. The left aSTS was identified as being selective for intelligible speech, as the contrast between the two rotated vs. the two unrotated (and unintelligible) conditions was significant for this region.

Findings by Belin and colleagues (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Belin, Zatorre, & Ahad, 2002) also support a specialization for speech sounds for the left aSTS. The right aSTS, however, seems to be more sensitive to vocal sounds in general, including non-speech vocalizations like laughter and crying, than to speech in particular. One PET study (Belin et al., 2000) found a small region in the bilateral STS to be more activated by vocalizations than by environmental sounds, but for the aSTS, a significant effect was detected only in the right hemisphere. In a later fMRI study (Belin et al., 2002), the upper bank of right and left aSTS responded significantly more strongly to vocalizations than to environmental sounds; still, the effect was more pronounced in the right hemisphere. The second experiment in this study compared speech and non-speech vocalizations with their scrambled versions. These scrambled stimuli had the same amplitude envelope and the same spectrum of frequencies as the original items, but the energy distribution over frequencies was altered every 12ms, so that the spectral peaks were neither those of the vocal stimuli nor continuous. Scrambled voices are unrecognizable. The activation elicited by speech was stronger than that elicited by all other stimuli in the bilateral aSTS as well as in almost all other highly voice-sensitive sites identified in the first experiment. When speech was contrasted with its scrambled version, an effect showed in the bilateral STS, but it was stronger in the left hemisphere. Conversely, the difference between non-speech vocalizations and scrambled vocalizations was significant in the right aSTS only. While these results

do not rule out the possibility that the left aSTS also responds to stimuli other than speech, it shows that this area strongly prefers speech to the other stimulus types tested so far.

While the aSTG, too, seems to be more sensitive to speech than to other sounds, it nonetheless has been shown to respond to different types of auditory stimuli, as well. Zatorre, Evans, Myer, & Gjedde (1992) detected left aSTG activation not only when subjects listened to spoken syllables, but also when they heard noise bursts with durations, amplitude envelopes, and spectral shapes resembling those of the speech stimuli. When the activation for speech and noise was compared, no difference was found in the left aSTG, although the right aSTG was sensitive to this distinction. In another PET study, Zatorre and Belin (2001) presented only tones to their subjects and still found activation in the bilateral aSTG. The stimuli consisted of series of pure tones. In one condition, the alternation rate was varied while only two different frequencies were used. In the other condition, the tones switched at the same rate, but the number of frequencies used was varied. Although left and right aSTG were sensitive to both manipulations, the left aSTG activity correlated more with the alternation rate, i.e. the temporal variation, while the activity of the right aSTG correlated more with the number of frequencies used.

This finding corroborated Zatorre and Belin's hypothesis of an advantage for temporal information in the left aSTG as the left hemisphere is dominant for language and temporal information plays a critical role in speech perception (Shannon, Zeng, Kamath, Wygonsky, & Ecelid, 1995). The right hemisphere, on the other hand, is considered to be specialized for pitch processing (Zatorre, 2001), which relies on the analysis of acoustic frequencies.

The experimental results thus support the idea that the left aSTL is more sensitive to speech than to other auditory stimuli, without necessarily being exclusively engaged in language processing. Yet, not all experiments using speech stimuli have reported aSTL activation. Binder et al. (1994), for example, found only patchy activity of the aSTG/aSTS for the perception of words and sentences. In another study (Binder, Frost, Hammeke, Rao, & Cox, 1996), a difference in aSTS activation between word comprehension and tone perception was task dependent: It was found only when a semantic or pitch decision had to be performed on the stimuli, but not under a passive listening condition, when the differential activation did not reliably extend beyond the middle part of the STS/STG.

There are a number of possible reasons for the absence of reliable aSTL activation in speech processing experiments. One problem is that there seems to be considerable interindividual variation with respect to the precise STS location that responds to speech. In the Belin et al. (2002) study, for example, seven out of eight subjects had maxima of vocalization sensitivity in the upper bank of the STS, but the location differed widely along the horizontal dimension (right: $y=-6$ to $y=-41$; left: $y=-14$ to $y=-46$, in millimeters in stereotaxic space; Talairach & Tournoux, 1988). If there is only partial overlap between the subjects' regions of activation, the detection of reliable effects is obviously difficult.

Another problem is inherent to the fMRI technique: The signal coming from tissue close to bone or air-filled cavities can be lost or distorted due to magnetic field inhomogeneities, and the anterior temporal lobe is an area that is particularly prone to these susceptibility artifacts (Gorno-Tempini et al., 2002). PET, however, is not subject to these limitations (Johnsrude, Giraud, & Frackowiak, 2002).

Finally, in some cases a signal might simply remain below the threshold of statistical significance. If aSTL activation depends on the complexity and difficulty of stimuli and task, not all tasks and materials to which the aSTL is potentially sensitive might engender activation that is strong enough to be detected reliably. Likewise, differences in acoustic complexity and task demands can be responsible for differential activation in two conditions, reflecting quantitative differences, i.e. degrees of involvement, rather than qualitative ones, such as strict selectivity for a particular type of material.

ASTL as Sensory Association Cortex

Some of the authors who found aSTL activation speech perception undertook to integrate their results with ideas of auditory cortex organization in primates and humans. The auditory cortex is typified by a hierarchical organization as well as distinction between two processing streams (Pandya, 1995; Rauschecker, 1998; Romanski et al., 1999). Binder et al. (2000) and Scott et al. (2000) proposed that the aSTL areas they had found to be activated by speech stimuli should be regarded as part of auditory association cortex with complex and specific response properties. Scott et al. (2000) additionally suggested that the aSTS area that was activated by intelligible speech is associated with the anterolateral auditory processing stream that is engaged in sound recognition.

Primate auditory cortex consists of three hierarchically organized parts (Kaas & Hackett, 2000). The first stage of processing occurs in the auditory core, which is located on the temporal plane within the Sylvian fissure. It consists of three areas, A1, R, and RT, all of which possess functional and cytoarchitectonic features of primary sensory cortex. Neurons in these areas are organized in a tonotopic fashion and show maximal sensitivity to pure tones. The core areas are connected with each other as well as with the surrounding areas that constitute secondary auditory cortex, the auditory belt. The core has no ipsilateral long distance connections that are not relayed by the belt. Neurons in the belt areas are tuned not to pure tones, but to narrow frequency bands, and are particularly sensitive to frequency modulations. The belt areas are reciprocally connected with each other, with the core, and with adjacent areas of tertiary auditory cortex, namely the parabelt on the lateral STG surface. With the distance from the auditory core increases the complexity of the functional properties; neurons in the parabelt respond selectively to complex auditory stimuli, such as combinations of tones in a certain order or particular vocalizations (Rauschecker, 1998). Parabelt areas subsequently project to temporal and frontal cortices. Many of these connections target the upper and lower bank of the STS (Kaas & Hackett, 2000), which in addition receives input from different modalities (Seltzer & Pandya, 1986).

While most of the literature on auditory cortex organization is based on data from non-human primates, studies using anatomical (Hackett, Preuss, & Kaas, 2001; Wallace, Johnston, & Palmer, 2002) as well as functional imaging methods (Wessinger et al., 2001) have provided some evidence for a similar organization in the human auditory system. Assuming that the human auditory cortex is organized in this hierarchical manner, Binder et al. (2000) suggested that the ventral STG/STS area that responded to speech could be part of the higher order auditory cortex, as it is presumed to process complex stimuli and to respond to combinations of features. Scott et al. (2000) related the selectivity for speech they found in the left aSTS to neurons in primate auditory association cortex that are specialized for species-specific vocalizations (Rauschecker, 1998).

In addition to levels in this processing hierarchy, a distinction between a ventral/anterior and a dorsal/posterior processing stream has been proposed (e.g., Romanski et al. 1999). Both originate in the auditory core, are relayed by distinct areas in belt, parabelt, and temporal or parietal cortex, and target different prefrontal areas. In analogy to visual

pathways (Ungerleider & Haxby, 1994), the anterior and posterior systems are usually thought of as 'what' and 'where' streams, recognizing and localizing sounds, respectively (Romanski et al., 1998). An alternative proposal for the posterior stream is that it processes spectral movement, i.e. changes in the frequency spectrum (Belin & Zatorre, 2000). Functional neuroimaging studies and the examination of patients with anterior and posterior lesions including portions of the temporal lobe have also provided evidence for the existence of dual pathways in the human auditory system (Alain et al., 2001; Clarke et al., 2002).

As the aSTL is part of the anterior pathway (Rauschecker, 1998), it appears plausible that the aSTL is involved in the processing of complex auditory patterns. However, aSTL function cannot be explained solely in terms of auditory processing, since Stowe et al. (1998, 1999) reported aSTL activation for visually presented sentences as well. Without abandoning the idea that the aSTL is primarily an auditory area, one can find potential reasons for aSTL activation in response visually presented linguistic stimuli.

One possible explanation for aSTL engagement by written language processing is that the read material is transformed into a phonological code, which is likely to involve resources that are usually devoted to auditory language processing. There is a great deal of evidence for phonological recoding in reading (e.g., Coltheart, Avons, & Trollope, 1990; Rayner, Pollatsek, & Binder, 1998; Van Orden, Johnston, & Hale, 1988), although its time course is still subject to debate (Daneman, Reingold, & Davidson, 1995).

Another factor that may help account for the sensitivity to both spoken and written language is the convergence of information from different senses in the STS/STG. Anatomical studies in primates have identified the STS as an area that receives inputs from different modalities (e.g., Seltzer & Pandya, 1986). Functional MRI studies in human subjects have found areas in the STS and/or STG to respond to auditory as well as visual stimuli (Bernstein et al., 2002; Calvert, 2001; Olson, Gatenby, & Gore, 2002), as well as other areas that are sensitive to auditory and somatosensory information (Foxe et al., 2002). Cross-modal properties, i.e. a superadditive response to congruous audio-visual speech stimulation as compared to auditory and visual stimulation alone, have been detected in the STS (Calvert, 2001). In all of these fMRI studies, the observed activation was restricted to the posterior and middle portions of STS and STG. Puce and Allison (1999; cited in Allison,

Puce, & McCarthy, 2000), however, recorded intracranial event-related potentials which demonstrated that neurons in the mid/anterior STS respond to mouth movements, but not to eye movements, showing sensitivity to visual input that is potentially related to phonological-auditory information.

Discussion and Conclusion

While the left aSTL is quite clearly involved in language comprehension, it does not seem to be specialized for sentence processing, as aSTL activation can be elicited by a variety of auditory stimuli that do not contain sentence-level information such as prosody or syntax. The aSTS responds to simple speech stimuli like syllables with phonetic content but no semantic, syntactic, or prosodic information (Giraud & Price, 2001), and the aSTG is even responsive to non-speech stimuli (Zatorre & Belin, 2001). An alternative account is therefore needed. One possible way of explaining the data from the studies reviewed in this paper is to consider the aSTL as a part of the anterior auditory processing stream that is involved in recognizing the content of acoustic stimuli. Not all acoustic stimuli, however, will engage the aSTL. Instead, the aSTG and especially the aSTS appear to be involved only when more complex features and feature combinations, which are typical of speech, have to be analyzed. Besides speech stimuli usually eliciting more aSTL activation than simple tones (Binder et al., 2000), the aSTG also responds more strongly to more complex tone patterns than to simple ones (Zatorre & Belin, 2001). Furthermore, visual information that can be recoded into a phonological-auditory representation can engender aSTL responses, as well.

In addition to stimulus complexity, task demands affect the amount of aSTL activation, too. The aSTL is more engaged as the task increases in difficulty. For instance, processing ungrammatical sentences or jabberwocky may be harder than processing grammatical sentences with regular words, which was reflected in the differential aSTG responses to these conditions (Meyer et al., 2000, 2002). Furthermore, activation was stronger when ungrammatical sentences had to be repaired, and not only detected (Meyer et al., 2000). In the studies by Wise et al. (2001) and Mummery et al. (1999), aSTS activation was found to correlate with the presentation rate of speech stimuli, which can be seen as an increase in task and/or stimulus complexity, as more information has to be processed in the same amount of time.

Stimulus and task complexity might also account for the instrumental role that the left aSTL plays in sentence processing. Not only does the aSTL show stronger responses to sentences than to words (Mazoyer et al., 1993), its integrity also seems to be essential for the comprehension of morphosyntactic information (Dronkers et al., 1996). Sentence comprehension requires the processing of the semantic, syntactic, and prosodic information of sentences, and an efficient analysis of acoustic information is vital to a successful implementation of these higher-level processes. In addition, the loss of acoustic information becomes more detrimental to comprehension as sentences increase in complexity, which was demonstrated by Dick et al. (2001). In this study, subjects listened to sentences that were compressed, masked by noise, or low pass filtered. All these acoustic distortions impaired sentence comprehension as compared to the comprehension of the same sentences without acoustic degradation. Simple active sentences, however, were relatively unaffected, while the syntactically complex object cleft sentences showed the largest effects. It seems that especially the processing of more complex sentence structures depends on an optimal acoustic analysis of speech input.

The left aSTL is well adapted to speech processing, as it is sensitive to the complex auditory information that characterizes speech. The aSTS in particular seems to be tuned to the acoustic properties of speech, which should optimize speech processing. Such a specialization does not necessarily entail, however, that the function of the aSTS is strictly domain-specific. Instead of implying selectivity for language, a specialization may occur at a sensory level (cf. Zatorre, Belin, & Penhune, 2002). The contribution of the aSTL to language processing may therefore consist of the most efficient analysis of acoustic speech properties, which is a prerequisite to the processing of more abstract language properties, such as lexical or morphosyntactic information.

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