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# THE BRAIN BASIS OF LANGUAGE PROCESSING: FROM STRUCTURE TO FUNCTION

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**Friederici AD.** The Brain Basis of Language Processing: From Structure to Function. *Physiol Rev* 91: 1357–1392, 2011; doi:10.1152/physrev.00006.2011.—Language processing is a trait of human species. The knowledge about its neurobiological basis has been increased considerably over the past decades. Different brain regions in the left and right hemisphere have been identified to support particular language functions. Networks involving the temporal cortex and the inferior frontal cortex with a clear left lateralization were shown to support syntactic processes, whereas less lateralized temporo-frontal networks subserve semantic processes. These networks have been substantiated both by functional as well as by structural connectivity data. Electrophysiological measures indicate that within these networks syntactic processes of local structure building precede the assignment of grammatical and semantic relations in a sentence. Suprasegmental prosodic information overtly available in the acoustic language input is processed predominantly in a temporo-frontal network in the right hemisphere associated with a clear electrophysiological marker. Studies with patients suffering from lesions in the corpus callosum reveal that the posterior portion of this structure plays a crucial role in the interaction of syntactic and prosodic information during language processing.

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> Our words are bound by an invisible grammar which is embedded in the brain.
> Jonah Lehrer, in *Proust Was a Neuroscientist.*

## I. INTRODUCTION

Since the first discovery that language functions are directly related to brain tissue (28, 161, 258), people have been interested in understanding the neural basis of language. Starting with these early lesion studies, the advent of new methodologies such as electroencephalography (EEG), magnetoencephalography (MEG), and magnet resonance imaging (MRI), which can be used in vivo to image cognitive functions in the brain (fMRI) as well as gray matter anatomy and white matter fiber tracts (diffusion-weighted MRI), has lead to a considerable increase in brain-based language studies (for recent reviews, see Refs. 15, 208, 251).

Despite the fact that there are hundreds of studies on the topic, the description of the neural basis of language and speech still remains difficult. It is hard to see the wood through the trees. In the last decade, various models have proposed various paths through the wood (21, 67, 102, 117, 118). Although different in their perspective, there is a considerable and "hope-making" overlap of the different paths through the wood taken by the various models. Some models primarily focus on the neuroanatomy of speech perception (118, 213), whereas others try to specify the functional neuroanatomy of semantic and syntactic processes as well as the time course of these (21, 67). Yet others have considered different memory systems (247) or memory and control systems (102) as major parts of language processing. Taken together, however, these models seem to cover the different components of a language processing system quite well.

The goal of the present article is to describe the structural and functional neural network underlying sentence comprehension and how this process evolves over time as a sentence is perceived. We start the review by briefly sketching the time course of the different subprocesses constituting the process of sentence comprehension. Then, the general network underlying language function in the perisylvian cortex will be defined and its neuroanatomical architecture will be specified. Based on this background, the different processes taking place during comprehension, such as acoustic-phonological analyses as well as syntactic and semantic processes, will be described. These processes are hierarchically structured in time from the analysis of the auditory input to final integration and sentence comprehension. While auditory analyses clearly take place in the auditory cortices in the temporal lobes bilaterally, syntactic and semantic processes are supported by separable temporo-frontal networks strongly lateralized to the left hemisphere (LH) for syntax and less so for semantics. Processing of sentence-level prosody is supported by a temporo-frontal network in the right hemisphere (RH). These different processes and their respective neural implementation will be discussed at the neuroanatomical macro-level, and whenever possible also with respect to the neural structure at the micro-level considering cytoarchitectonics and receptorarchitectonics of the language-relevant cortices.

This review should be considered a critical one, but the goal is not to attack the position of single researchers. Rather, it is an attempt to provide a convergent view of what we know about the functional neuroanatomy of language up to now and what recent debates focus on.

The review will mainly focus on neuroimaging studies (fMRI, EEG, MEG) and will not include full coverage of all patient studies on language processing, although patient work is considered. This decision was taken based on the fact that lesion data are not always restricted to small circumscribed brain regions, and, moreover, on the finding that performance depends on the time of lesion onset and on plastic reorganization of language functions that may have occurred.

## II. A BRIEF VIEW OF SENTENCE PROCESSING

The present description of sentence processing crucially differentiates three linguistic processing phases after an initial phase of acoustic-phonological analysis (67). In a first sentence-level processing phase, the local phrase structure is built on the basis of word category information. In the second phase, syntactic and semantic relations in the sentence are computed. These involve the computation of the relations between the verb and its arguments, thereby leading to the assignment of thematic roles (i.e., the analysis of who is doing what to whom). Once both semantic and syntactic information lead to the compatible interpretation, comprehension can easily take place. For example, the interpretation of an animate noun in sentence initial position as in "Mary cuts the flowers" is easy, as a person is a likely actor. For sentences in which semantic and syntactic information do not easily map, the processing system might need an additional third phase during which a final consideration and integration of the different information types is achieved, possibly including the context or world knowledge. During auditory sentence processing, these three different phases interact with linguistic prosody providing, for example, information about phrase boundaries relevant for syntactic processes. Linguistic prosody can also signal what is in the thematic focus of a sentence (indicated by stress in German and other Indo-European languages) and whether an utterance is a declarative sentence or a question (indicated by pitch in German and other Indo-European languages). This information is either essential or modulatory to the syntactic and semantic processes in a given sentence.

The above description of the process of language understanding is certainly only a sketch of what psycholinguistics have to say about this very complex process, but it entails the basic processes that have to be considered when characterizing the neural basis of language comprehension.

## III. THE LANGUAGE NETWORK

From different overviews (67, 118, 251), it is clear that the language-relevant cortex includes Broca's area in the inferior frontal gyrus (IFG), Wernicke's area in the superior temporal gyrus (STG), as well as parts of the middle temporal gyrus (MTG) and the inferior parietal and angular gyrus in the parietal lobe (see **FIG. 1**). Within these macroanatomically defined regions, microanatomical subregions can be specified.

### A. Parcellation of the Language Cortex

Korbian Brodmann (29) was the first to provide a cytoarchitectonic description of the human cortex. Novel neuroarchitectonic approaches provide detailed information about subdivisions of regions of the language network. These new neuroarchitectonic approaches are *1*) advanced objective cytoarchitectonic analysis based on the density of different types of neurons in the cortex (5, 6), *2*) receptorarchitectonic analysis based on the distribution of different types of neuroreceptors in the cortex (3, 267), and *3*) the connectivity-based parcellation approach that subdivides brain regions according to their area-specific connectivity to other areas in the brain (8, 132).

Interestingly, all these approaches propose a subdivision of Broca's area itself, and segregate it from adjacent areas. This appears to be of importance as the larger region of Broca's area has often been discussed as supporting different aspects of language processing (20, 102, 207). Broca's area is usually defined as consisting of the cytoarchitectonically defined Brodmann area (BA) 44, the pars opercularis and BA 45, and the pars triangularis (5, 29) (see **FIG. 1**). Receptorarchitectonically, area 45 can be subdivided into two portions, a more anterior area 45a bordering BA 47 and a more posterior area 45p bordering BA 44 (3) (see **FIG. 2**). Moreover, area 44 can be receptorarchitectonically subdivided into a dorsal (44d) and a ventral (44v) area. These subdivisions may be of particular functional importance as different language experiments have allocated different functions to area

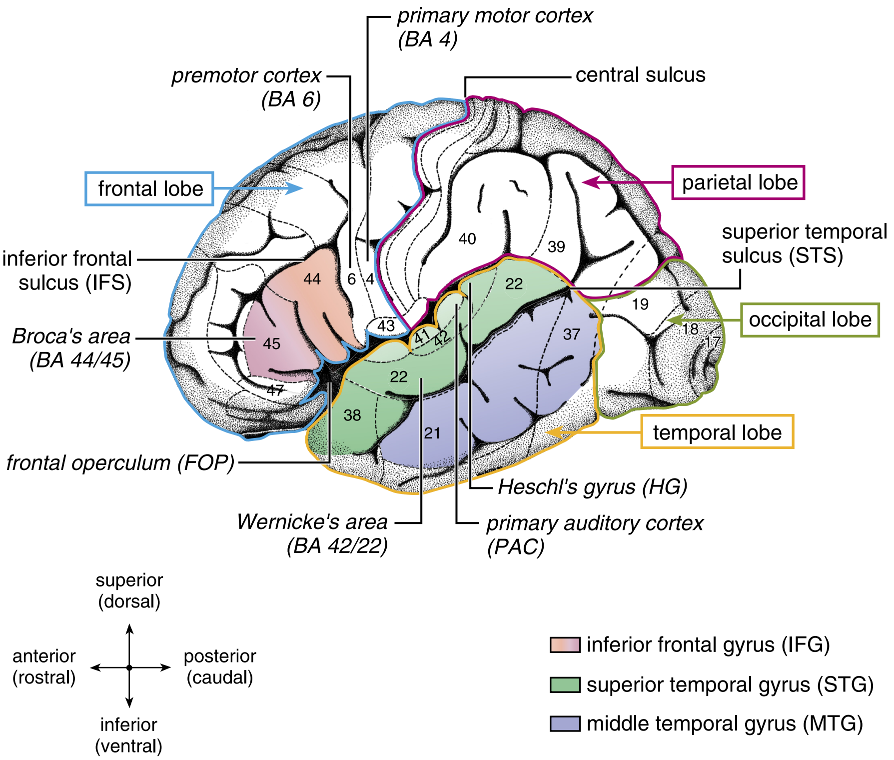

**FIGURE 1.** Anatomical and cytoarchitectonic details of the left hemisphere. The different lobes (frontal, temporal, parietal, occipital) are marked by colored borders. Major language relevant gyri (IFG, STG, MTG) are color coded. Numbers indicate language-relevant Brodmann Areas (BA) which Brodmann (1909) defined on the basis of cytoarchitectonic characteristics. The coordinate labels superior/inferior indicate the position of the gyrus within a lobe (e.g., superior temporal gyrus) or within a BA (e.g., superior BA 44; the superior/inferior dimension is also labeled dorsal/ventral). The coordinate labels anterior/posterior indicate the position within a gyrus (e.g., anterior superior temporal gyrus; the anterior/posterior dimension is also labeled rostral/caudal). Broca's area consists of the pars opercularis (BA 44) and the pars triangularis (BA 45). Located anterior to Broca's area is the pars orbitalis (BA 47). The frontal operculum (FOP) is located ventrally and more medially to BA 44, BA 45. The premotor cortex is located in BA 6. Wernicke's area is defined as BA 42 and BA 22. The primary auditory cortex (PAC) and Heschl's gyrus (HG) are located in a lateral to medial orientation.

45, and also to area 44 which now can possibly be assigned to different subregions within 45 (45a versus 45p) and 44 (44d versus 44v) when considering the more fine-grained neuroanatomic parcellation of this area (compare with sect. IVC2).[1]

With the use of a connectivity based approach, the IFG has been shown to separate into a subregion (BA 44) connecting to the temporal cortex via a dorsal pathway [which includes the arcuate fasciculus (AF) and the superior longitudinal fasciculus (SLF)], a second region anterior to it (BA 45) connecting to the temporal cortex via the extreme fiber capsule system (EFCS) and a third region located more ventrally (frontal operculum, FOP) connecting via the uncinate fasciculus (UF) to the anterior temporal cortex (8). This latter article shows that there is variance between subjects with respect to the absolute localization of each area, but it also reveals that the relative location of the three areas is stable across different subjects [see also Klein et al. (141) for a connectivity-based parcellation of the separation of BA 44 and BA 45 and their probabilistic overlap].

The microanatomical description of the auditory and temporal cortices provides the following picture. In the primary auditory cortex (BA 41 in **FIG. 1**), cytoarchitectonic analyses have revealed different subregions in a medial-to-lateral direction (with Te1.0 in the middle, Te1.1 more medially located, and Te1.2 more laterally located) (176). The cytoarchitectonically defined region BA 22 covers the posterior two-thirds of the lateral convexity of the STG (29) (see **FIG. 1**). Receptor and cytoarchitectonic subdivisions have proposed a separation of the dorsal and ventral banks of the STG (175). It is suggested that the lateral STG proper excluding the dorsal

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[1] It should be noted that these receptorarchitectonic analyses are performed in post mortem brains and thus represent an analysis of the brain's neuron receptors at a certain point in time. However, it is known that the density of neuron receptors is subject to dynamic modulations over a millisecond time scale. Moreover, we should keep in mind that up to now the functional relation between particular neuron receptors and particular language functions is not known.

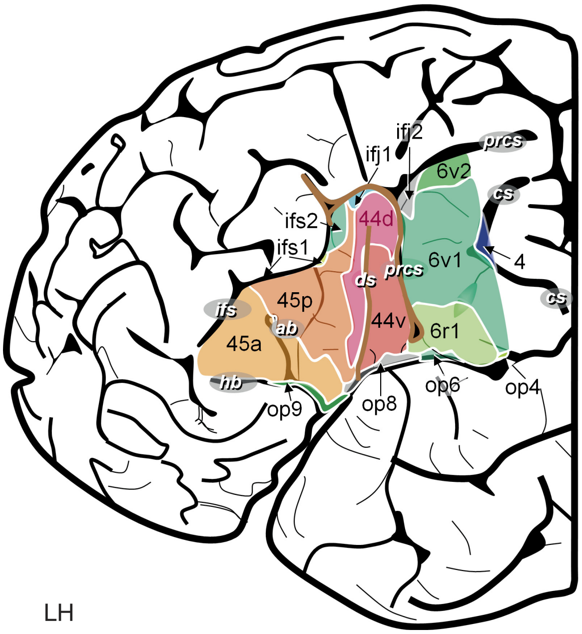

**FIGURE 2.** Receptorarchitectonic parcellation of the left posterior prefrontal cortex. Extent of delineated areas projected to the lateral surface of an individual post mortem brain. The following receptor binding sites were studied by Amunts et al. (3) for the prefrontal cortex: glutamatergic AMPA and kainite receptors, GABAergic $GABA_A$ receptors, cholinergic muscarinic $M_1$ and $M_2$ receptors, and noradrenergic receptors. The color coding indicates receptorarchitectonically defined borders. The borders between 44 d (dorsal) and 44 v (ventral), for example, were differentiated mainly by $\alpha_1$ and muscarinic $M_2$ receptors. Area 45 can be subdivided receptorarchitectonically into an anterior (45a) and a posterior (45p) part. Area 6 can be subdivided into three subparts. op, Operculum (numbering indicates different subparts); ifs, inferior frontal sulcus; ifj, inferior frontal junction; prcs, precentral sulcus; cs, central sulcus. [From Amunts et al. (3).]

and ventral banks is a functionally relevant area for language processing in humans. In the anterior-posterior dimension, there is no cytoarchitectonic parcellation of BA 22 as it covers most of the STG, except its most anterior portion (BA 38) (see **FIG. 1**).

As the cyto- and receptorachitectonic analysis cannot be conducted in the living brain, the team working with these approaches has calculated "probability maps" from post mortem brains of which the cytoarchitectonic analyses are available online (http://www.fz-juelich.de/inm/index.php?index=51).

## B. Structural Connections Between the Language Cortices

The identification of fiber pathways between Broca's area and the temporal cortex (Wernicke's area) dates back to the late 19th century when Dejerine (47) defined the arcuate fasciculus as the dominant fiber tract connecting these two regions. Nowadays, diffusion tensor imaging (DTI) allows the identification of structural connections between different brain regions in the human in vivo (e.g., Refs. 11, 132). For a recent tractography atlas representing the major fiber connections based on this method, see Catani and de Schotten (38). Note, however, that with this approach the directionality of the connection cannot be determined. Concerning the connection between the language-relevant regions, i.e., the (pre)frontal cortex and the temporal cortex, the literature generally agrees on two pathways, a dorsal and a ventral pathway. Recently, there has been debate with respect to the particular functions of different pathways from the temporal cortex to other parts of the brain as well as with respect to their end points in the other brain regions (see Refs. 65, 66, 256) (see **FIG. 3**).

Within "dual stream models" (117, 118, 213), the ventral pathway has been taken to support sound-to-meaning mapping, whereas the dorsal pathway connecting the posterior dorsal-most aspect of the temporal lobe and the posterior frontal lobe has been suggested to support auditory-motor integration (118). Using a deterministic fiber tracking approach in which the two end points of the connection are predefined on the basis of functional data, Saur and coworkers (227, 228) interpret the ventral pathway connecting the temporal cortex with the pars orbitalis (BA 47) and triangularis (BA 45) via the EFCS as supporting sound-to-meaning mapping, and define the dorsal pathway as going

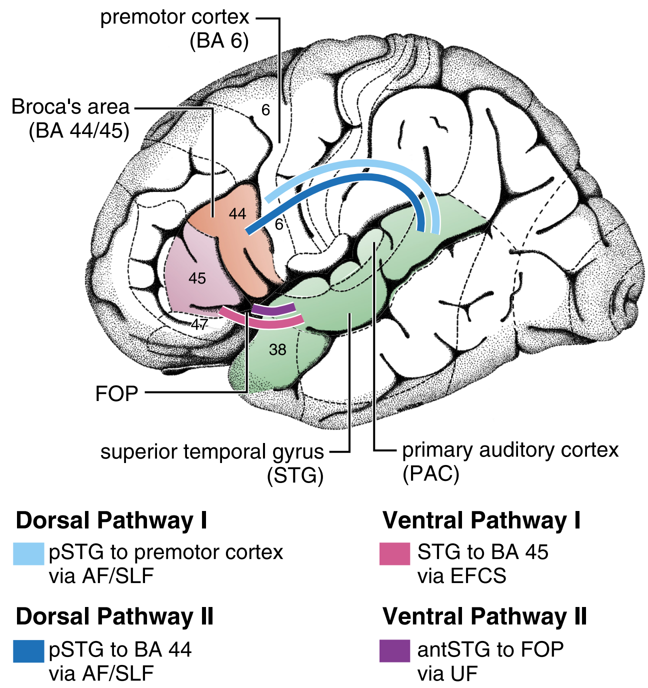

**FIGURE 3.** Structural connectivities between the language cortices. Schematic view of two dorsal pathways and two ventral pathways. Dorsal pathway I connects the superior temporal gyrus (STG) to the premotor cortex via the arcuate fascile (AF) and the superior longitudinal fascicle (SLF). Dorsal pathway II connects the STG to BA 44 via the AF/SLF. Ventral pathway I connects BA 45 and the temporal cortex via the extreme fiber capsule system (EFCS). Ventral pathway II connects the frontal operculum (FOP) and the anterior temporal STG/STS via the uncinate fascile (UF).

from the temporal lobe to the premotor cortex and continuing to the pars opercularis (BA 44) supporting sensory-motor mapping of sound-to-articulation. This functional interpretation stands in slight contrast to probabilistic fiber tracking approach in which only one end of the connection is defined as a seed point. Defining two seed points in the IFG on the basis of two functionally different activations, Friederici et al. (69) identified a dorsal pathway going from pars opercularis (BA 44) to the posterior temporal cortex via the AF/SLF, and a ventral pathway from the FOP via the UF to the anterior temporal cortex. The function of the dorsal pathway was seen in the support of processing non-adjacent elements in syntactically complex sentences and the ventral pathway taken to support combinations of adjacent elements in a sequence.

Thus these findings as well as additional data from intraoperative deep stimulation (56) make it likely that there are two ventral pathways connecting the frontal to the temporal cortex involved in language processing, one from BA 45 via the EFCS to the temporal cortex (ventral pathway I) and one from the FOP via the UF (ventral pathway II). Moreover, there is suggestive evidence that there are two parallel dorsal pathways, one from the temporal cortex to the premotor cortex (dorsal pathway I) and one from the temporal cortex to BA 44 (dorsal pathway II), with the former mainly supporting sound-to-motor mapping and the latter supporting higher-level language processes (see Ref. 39, and for a recent debate, see Refs. 65, 66, 256).

This subdivision into two dorsal pathways is in line with recent structural connectivity data from very young infants showing a dorsal fiber tract from the temporal lobe going only to the motor/premotor cortex (55). This pathway (dorsal pathway I) subserving auditory-motor integration is already of primary importance during early language acquisition, when tuning the system towards the target language (118). A dorsal fiber tract that connects the temporal lobe with Broca's area in the IFG (dorsal pathway II) develops much later and appears to be functionally related to higher-level semantic and syntactic language functions (26). It is an open issue whether these dorsal connections are direct or indirect with an intermediate stage in the inferior parietal cortex (39, 212, 213) whose role within the dorsal stream might be that of phonological working memory storage (198, 245).

In addition to these long-range connections, functional connectivity and structural connectivity analyses, moreover, have identified two short-range pathways within the temporal cortex, a first one from Heschl's gyrus (HG) to the planum polare and anterior STG via a rostral fiber pathway and a second one from HG to the planum temporale (PT) and posterior STG via a caudal fiber pathway (248). These data suggest two auditory processing streams within the temporal cortex: 1) between the primary auditory cortex (PAC) and the anterior auditory cortex (planum polare) and 2) between the PAC and posterior auditory cortex (planum temporale). Short-range connections have also been reported for the prefrontal cortex, interconnecting the inferior frontal sulcus and BA 44 (166).

To summarize, in addition to short-range structural connections within the language-related cortex, there are multiple long-range structural connections between the language-relevant regions in the frontal and temporal cortices: two dorsal pathways and possibly two parallel ventral pathways. Although the direction of the connectivity cannot be determined in humans using the DTI approach, data from animal studies using invasive tracer methods suggest strong directionality from sensory regions to the prefrontal cortex in the monkey (101, 221). The reverse information flow is also considered, and the two directions are discussed in terms of feed-forward and backward projections (212). In the domain of human language processing, projections from sensory to the premotor cortex (via dorsal pathway I) could support bottom-up information processes, whereas projections from Broca's area to the temporal context (via dorsal pathway II) could subserve top-down processes drawing prediction about the incoming information, thereby easing its integration. Further research must show whether these assumptions for language processing hold.

The precise function of these structural connections, however, can only be defined indirectly, namely based on the function of the particular regions they connect. One way to establish a closer relation between structural and functional information might be to use the anatomical connectivity as a prior for dynamic causal modeling of fMRI data (240).

## C. Functional Connections in the Default Language Network

Every brain-based study on language processing reports at least one function-related activation in the left perisylvian cortex, which includes the prefrontal, frontal, temporal, and parietal cortices. The particular function assigned to a given area in the perisylvian cortex as defined on the basis of functional imaging studies investigating different aspects of language processing, such as phonology, syntax, and semantics, will be discussed in detail in section **IV**.

Here we will first consider recent data which suggest that the experimental variations in these studies only reflect the tip of the iceberg, since specific experimental conditions can only explain ~20% or less of the total variance of the activation of the brain in a given experiment (162). The rest of the variance represents activation not induced by the specific experimental conditions. Interestingly, this "unexplained" activity is not random. For language experiments, it is located in the perisylvian cortex. As this activation pattern was only observed for language experiments and not for nonlanguage experiments, it was taken to represent the default language network (162). To identify this default activation, a low-frequency fluctuation analysis of fMRI data compared four language experiments with two nonlanguage experiments from the same laboratory (for method, see Ref. 162; for low-frequency fluctuation analysis in general, see Refs. 17, 211).[2] Moreover, when conducting a functional connectivity analysis within this default language network, a significant correlational connectivity was found between Broca's area in the IFG and the posterior superior temporal lobe (162) (see **FIG. 4**).

Thus it is already within the default language network that there are functional connections between different language regions, independent of the different conditions induced by a given experiment. To summarize, the particular activation pattern reported for specific experimental conditions aiming to test semantic or syntactic processes as reported in the different language fMRI studies thus only represents a modulation of this default language network.

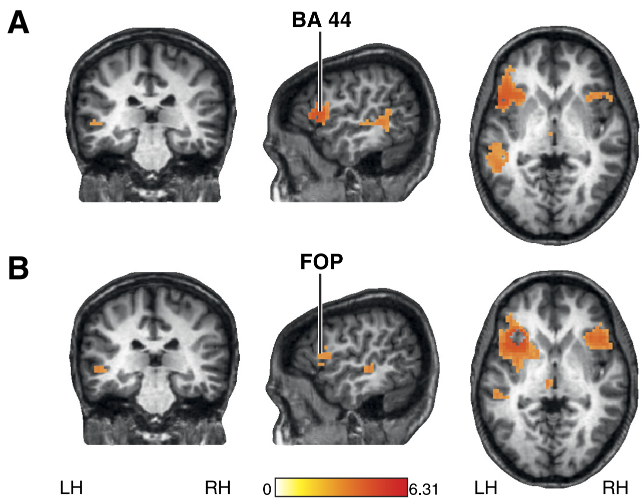

**FIGURE 4.** Functional connectivities between the language cortices within the default language network. Results are of a conjunction analysis involving 4 language experiments corrected for multiple comparisons using FDR thresholded at $P < 0.05$. *A*: correlations with the seed region BA 44. *B*: correlations with the seed region in FOP. For each experiment, the correlations were *r*-to-*z* transformed to ensure Gaussianity and then subjected to a voxelwise *t*-test across subjects. The map shows the *z* values for the conjunction of all 4 language studies. The *z* values are color coded as indicated by the color bar. [Adapted from Lohmann et al. (162), by permission of Oxford University Press.]

## IV. PROCESS-SPECIFIC NEURAL NETWORKS

Spoken sentence comprehension requires a number of subprocesses to derive the meaning of a sentence from the auditory input, as there are acoustic-phonological, syntactic, and semantic processes. We will discuss the brain regions supporting these different processes in turn.[3]

### A. Acoustic-Phonological Analysis

The comprehension of spoken language starts with the acoustic-phonological analysis of the speech input. The obvious neural candidate to support this process is the auditory cortex and adjacent areas.

In an attempt to specify subregions in the auditory cortex and adjacent areas in humans, researchers have relied on neuroanatomical data from non-human primates for which a core region in HG, a surrounding belt and parabelt region has been identified (213, 230). In humans, the PAC is located on the superior surface of the temporal lobe bilaterally in HG. Three regions can be identified adjacent to HG. A region located posterior, the planum temporale (PT), a region anterolateral to HG called planum polare (PP), and a region at the lateral convexity of the cortex in the STG extending to the superior temporal sulcus (STS). All these regions are involved in the acoustic analysis of speech. Cytoarchitectonic studies have indicated that the PAC usually covers the medial two-thirds of the anterior HG (176), and the identification of a subregion in the lateral convexity of the STG has been confirmed by a receptorarchitectonic analysis (175).

Functionally, a primary step is to differentiate speech from nonspeech acoustic signals, and for a description of the neuroanatomic basis of speech comprehension, it would be of major interest to identify where in the processing stream this takes place. The primary auditory analysis is computed in HG. Functional neuroimaging studies show that HG is activated by any type of sound (133, 177). The region lateral to HG at the convexity of the STG extending into the STS has been found to respond to acoustic features of phonetic parameters (16), but also to variations of frequency and spectral information in nonspeech sounds (109) and is thus not specialized for speech. Functional imaging studies have, moreover, shown that PT also does not react specifically to speech sounds, at least compared with equally complex nonspeech sounds (48, 261, 266). The infor-

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[2] Earlier studies using the method of low-frequency fluctuation analysis identified a general default network while subjects rested quietly in the scanner (17, 211). With data from such a resting state, functional connectivities between different subregions of the IFG (i.e., pars orbitalis, pars triangularis, and pars opercularis) and subregions in the parietal cortex and temporal cortex have been reported (263).

[3] Note that the anatomic terminology varies from study to study. Here we used those anatomic terms provided by the authors of the study discussed. **FIGURE 1** may help to orient the reader with respect to the different anatomic terms.

mation flow from HG to PT has been demonstrated in a time-sensitive fMRI paradigm, indicating the involvement of HG and PT at different points in time (264). It has been concluded that HG is associated with analyzing the sound signal per se, whereas the PT may be involved in categorizational processes. The PT has been proposed as the region for the segregation and matching of spectrotemporal patterns and as serving as a "computational hub" gating the information to higher-order cortical areas (95).

Speech perception of phonemes (consonants) was found to activate a region anterolateral to HG in the STG/STS (189). This region differentiates between speech and nonspeech sounds. In contrast, the left posterior STG was found to process the basic acoustic characteristics of the signal. Given their respective responsibilities, the posterior STG was defined as reflecting earlier processes than the anterolateral STG/STS (146). The fMRI finding that the posterior STG houses an earlier processing level than the anterolateral STG/STS is consistent with magnetoencephalographic evidence locating the relatively early N100 response to consonants in HG and PT (188) and with patient evidence showing that lesions in the posterior STG lead to word deafness as well as deficits in the perception of nonspeech sounds (204). Other neuroimaging studies, however, reported the PT or the supramaginal gyrus to respond to speech compared with nonspeech sounds (46, 131, 174). These studies, in contrast to Obleser et al. (189), who used a passive listening paradigm, used attention-demanding tasks. From these data, it appears that under specific task demands, the differentiation between speech and nonspeech sounds by means of top-down processes may be shifted to an earlier processing level, in this case the PT.

Functionally, PAC in the left and the right hemispheres are responding to speech and tonal pitch, but they appear to have different computational preferences, with the left PAC reacting specifically to speech sounds characteristics and the right PAC to characteristics of tonal pitch (265). The relative specialization of the two auditory cortices for these stimulus types, which differ in their temporal and spectral characteristics, is described as a specialization for rapidly changing information with a limited frequency resolution in the left hemisphere and a system with reverse characteristics in the right hemisphere. The former system would be ideal for the perception and recognition of speech sounds, as the determination of these (i.e., phonemes in a sequence) requires a system with a time resolution of 20–50 ms. The latter system would be able to deal with suprasegmental information (i.e., prosody requiring a system with a time resolution of 150–300 ms). Hickok and Poeppel (118) proposed that the left and right hemisphere generally work at different frequencies, leading to a relative lateralization of functions. The left hemisphere primarily works in gamma frequencies, whereas the right hemisphere works in the theta range (93).

When considering functional levels of speech perception, a next relevant level is "intelligibility" in its most general sense (i.e., language understanding including both semantic and syntactic processes). The methodological approach used to investigate processes at this level is the manipulation of the acoustic signal by spectrally rotating normal speech to render the speech signal unintelligible (18). Studies using such manipulations have consistently shown that the anterior STS is systematically activated as a function of intelligibility (see **TABLE 1**). The posterior STS, in contrast, was found to be equally activated by normal speech, rotated speech, and noise-vocoded speech (232), leading to the idea that this area is involved in the short-term representation of sequences of sounds that contain some phonetic information (without being necessarily intelligible) (229). This functional differentiation is interesting in the light of the two different pathways from the primary auditory cortex discussed in section III*B*, one going from HG to the anterior STS/STG and one going from HG to the posterior STS/STG (248). Moreover, these observations are in line with clinical studies on patients with focal cerebral disease in the anterior temporal regions showing deficient speech comprehension (1, 14, 89, 119, 182).

To summarize, as a first processing step during auditory language comprehension, the brain has to perform an acoustic analysis in an auditory cortical network starting at the PAC and then distributing the information in two directions, *1*) to the PT and posterior STG and *2*) to the planum polare and the anterior STG. As yet, little is known about the particular function of the planum polare in processing speech or complex nonspeech sounds. The PT has been

**Table 1.** *Activation in anterior temporal lobe as a function of intelligibility during speech perception*

| Study | Coordinates | Location |
|---|---|---|
| Scott et al. (2000) | [MNI] | |
| | −54, 6, −16 | L ant STS |
| Narain et al. (2003) | [Talairach] | |
| | −56, −6, −20 | L ant STS |
| Crinion et al. (2003) | [MNI] | |
| | −58, −6, −12 | L mid STS |
| Obleser et al. (2007) | [MNI] | |
| | −57, −6, −5 | L ant STS |
| Friederici et al. (2010) | [MNI] | |
| | −58, −4, 4 | L ant STS |
| Obleser and Kotz (2010) | [MNI] | |
| | −60, −8, −6 | L ant STS |

Coordinates ($x$, $y$, $z$) are given either according to Talairach or to MNI. L, left; ant, anterior; mid, middle; STS, superior temporal sulcus.

suggested as the "computational hub" from which information is gated to higher-order cortical regions (95). A connection from the temporal cortex to the premotor cortex appears to support auditory-to-motor mapping and has been claimed to represent part of the "phonological network" (228).

## B. Initial Syntactic Processes

Several psycholinguistic models have proposed that the sentence parser processes syntactic information at different levels with an initial stage during which the simplest syntactic structure based on word category information is constructed and a second stage during which the relations who is doing what to whom are established (63). These models called serial syntax-first models have been challenged by interactive and constraint-satisfaction models (163, 169), which assume that syntactic and semantic information interact at any time. Syntax-first models, however, receive some support from neurocognitive models of language comprehension, which consider event-related brain potentials (ERPs) to provide crucial information about the temporal structure of language processing (21, 67).

As syntax-first models assume that the important syntactic processes relevant for the assignment of the grammatical structure of a sentence to occur only a couple of hundred milliseconds later than the initial syntactic parse, it is not easy to separate these two stages of syntactic processing using fMRI due to the low temporal resolution of this method. One way to investigate the different syntactic stages is to introduce violations in natural sentences which tap either the initial or the later syntactic processing stage. The initial processing stage will clearly be affected by word category violations, since incorrect word category information would make the building up of an initial local phrase structure impossible while violations of grammatical relations in the sentence will affect a later processing stage. Another way of investigating local syntactic structure building is to use artificial grammars which lack semantic relations. Initial local phrase structure building processes[4] were found to be correlated with increased activation in the frontal operculum and the anterior STG both in studies on natural grammar processing (81) and on artificial grammar sequences (69). The natural grammar study in German introduced a word category error within a prepositional phrase by putting a verb instead of a noun after the preposition, e.g., "The pizza was in the eaten" instead of "The pizza was in the restaurant eaten" (literal translation). The past participle verb form is syntactically incorrect, disallowing local structure building. The artificial grammar experiment used a probabilistic grammar in which an element of the category A (a certain syllable type) was always followed by an element of the category B (another syllable type), e.g., ABABAB. A violation was created by having an A syllable followed by another A syllable in the sequence. The processing of this syntactic error in the artificial grammar sequence led to activation in the FOP. Taking the maximum of activation as a seed point for tractography analysis in each individual, a ventrally located fiber tract connecting the FOP and the anterior STG via the uncinate fasciculus was found (69). On the basis of this finding, it has been suggested that the FOP together with the anterior STG supports local structure building. More generally, this network could be viewed as the system that supports rule-based combinatorics of adjacent elements.

During sentence processing, this initial stage of phrase structure building is mandatory and should in principle be observable whenever a sentence is processed. Thus the FOP should be seen with increased activation not only for violations in sentences and sequences, but also when comparing sentences to nonstructured word lists. Activation of the FOP was observed in a study comparing sentences to word lists without function words (78), but not in other studies using mixed word lists. Most of these other studies used word lists that allowed local structure building partly due to syntactically legal combinations of two or three words in the list, for example, adjectives and nouns (125, 127, 236, 241, 250). Interestingly, Vandenberghe et al. (250) report activation in the FOP (−48, 22, 4) for different sentence conditions providing word category information compared with control conditions in which unpronounceable letter sequences (providing no word category information) were used. All these findings are thus generally in line with the view that local structure building is supported by the FOP. However, it should be noted that local structure building is quite automatic in adults only requiring small resources (as indicated by ERP studies; see sect. **V***B*). Therefore, the FOP may not be seen to be significantly activated in each study with native adult listeners. Moreover, given that the activation in native listeners is very small, significant activations may not be observable in grand averages across subjects due to the variability of the location of the FOP across individuals as shown in a connectivity-based parcellation study (8). Further research taking individual subject data into account must clarify this issue.

Studies investigating sentence processing under less proficient processing conditions as in language development (27) and second language learning (222) show that processing phrase structure violations involves the IFG, in particular Broca's area, and not just the FOP. This suggests that there may be a shift in the recruitment of necessary parts of the ventral prefrontal cortex for local syntactic structure building as a function of language proficiency.

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[4] The low temporal resolution of fMRI, however, will not allow us to differentiate early and late effects observed in the ERP in response to incorrect word category information (see sect. **V**, *B* and *C*), but in combination with ERP studies from patients with lesions in particular parts of the brain as well as MEG localization studies with healthy participants, conclusions about the localization of these effects are possible.