Towards a neural basis of auditory sentence processing

Angela D. Friederici

Functional dissociations within the neural basis of auditory sentence processing are difficult to specify because phonological, syntactic and semantic information are all involved when sentences are perceived. In this review I argue that sentence processing is supported by a temporo–frontal network. Within this network, temporal regions subserve aspects of identification and frontal regions the building of syntactic and semantic relations. Temporal analyses of brain activation within this network support syntax-first models because they reveal that building of syntactic structure precedes semantic processes and that these interact only during a later stage.

Angela D. Friederici
Max Planck Institute of Cognitive Neuroscience, PO Box 500 355, 04303 Leipzig, Germany.
e-mail: angelafr@cns.mpg.de

Listening to connected speech is a task that humans perform effortlessly each day. This is surprising given the short time that the processing system has to deal with different types of information. Segmental phonemes and suprasegmental phonological information (prosody or pitch) as well as syntactic and semantic information must be accessed and coordinated within milliseconds. With respect to syntactic and semantic processes, two alternative views have been proposed in psycholinguistic comprehension models. One view, which is characterized by serial or syntax-first models, holds that syntax is processed autonomously prior to semantic information [1,2]. A second view, represented by interactive or constraint-satisfaction models, claims that all types of information interact at each stage of language comprehension [3,4]. Both classes of models are supported by a number of sentence-reading studies that use different behavioral paradigms (for details see 1).

None of these models addresses explicitly the role of prosodic information that is available whenever spoken sentences are processed. Unfortunately, the few behavioral studies that have investigated possible interactions between prosodic and syntactic information during auditory language comprehension do not provide a unitary view: although some data indicate an interaction between prosodic and syntactic information [5,6], others do not [7].

These differences are attributable partly to the fact that different behavioral paradigms tap into different processing aspects (automatic versus

Box 1. Psycholinguistic models of language comprehension

Two main classes of models have been proposed to account for the behavioral data on language comprehension: serial, syntax-first and interactive, constraint-satisfaction models [a]. As these models are based on data from reading, they comprise semantic and syntactic processes but ignore prosodic processes. Serial, syntax-first models assume that the parser initially constructs the simplest syntactic structure on the basis of word-category information, independent of lexical-semantic information. The latter information is processed during a second stage that is responsible for thematic-role assignment. If the initial syntactic structure and the thematic structure cannot be mapped onto one another, reanalysis takes place [b–d].

Recent studies, however, indicate that, for ambiguous structures, the initial structure building is not totally independent of non-structural variables such as the frequency of a particular structure or the semantic plausibility associated with the main verb [e,f]. This has led to constraint-satisfaction models in which it is assumed that, in the case of structural ambiguities, multiple syntactic interpretations are generated and weighted according to nonstructural factors.

An influential interactive model that describes processes of auditory comprehension was formulated in 1980 [g]. In this model, syntactic and semantic processes interact from an early stage during auditory language comprehension. Experiments that focus on prosodic aspects indicate that this is also true for syntactic and prosodic processes [h].

Although in both classes of models syntactic and semantic information are integrated during language perception to achieve understanding, interaction takes place at different points during processing: interactive, constraint-based models predict early interaction, whereas serial, syntax-first models predict interaction during a later stage of processing.

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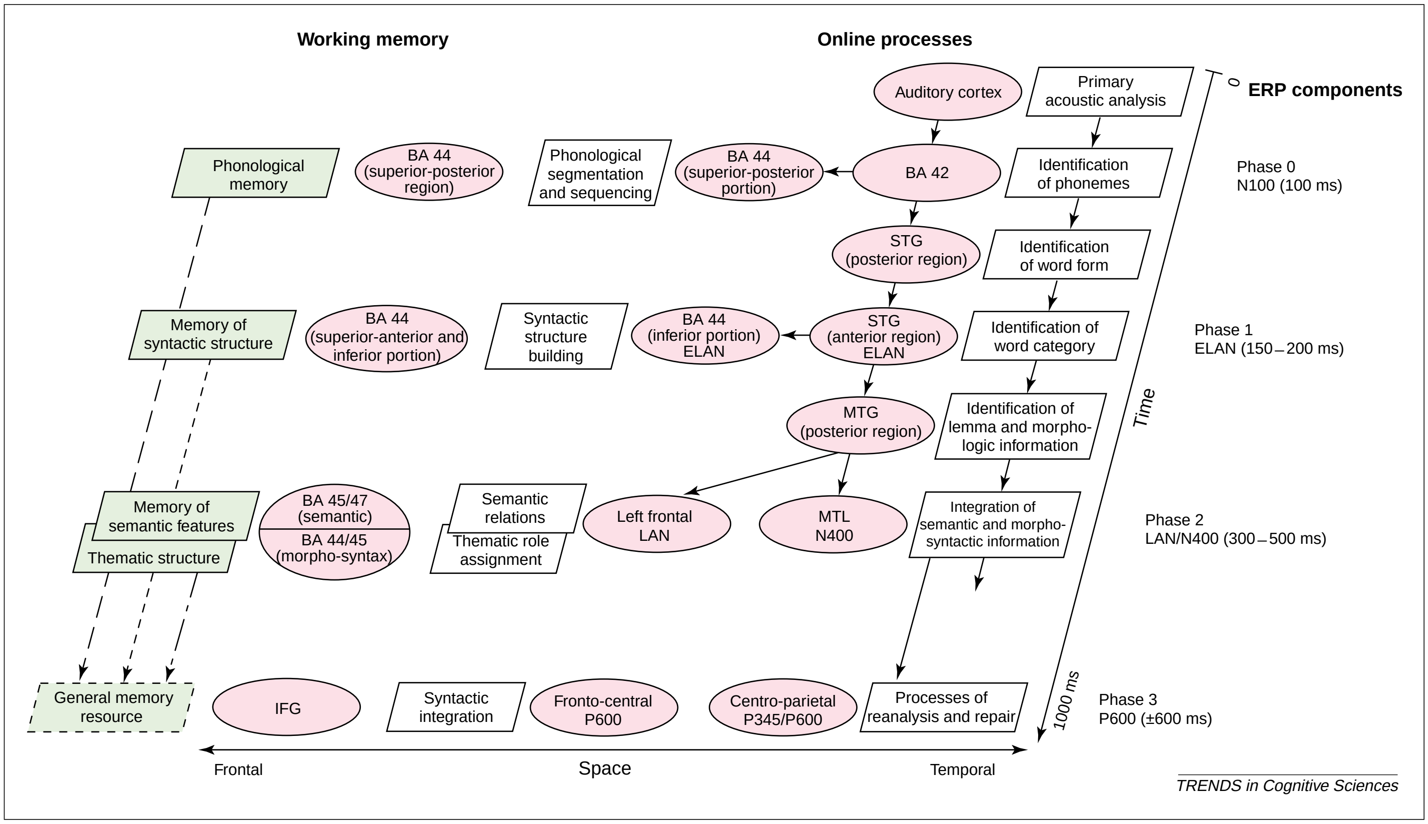

Fig. 1. Neurocognitive model of auditory sentence processing. The boxes represent the functional processes, the ellipses the underlying neural correlate identified either by fMRI, PET or ERPs. The neuroanatomical specification (indicated by text in square brackets) is based on either fMRI or PET data. The ERP components specified in their temporal structure (left-hand side) are assigned to their neural correlate by the function rather than the localization of their generator. This holds true for the ERP components of phase 2 and -3 as late components are hard to localize. The different distributions of the P600 and their functional nature are discussed in Ref. [53]. The neural correlate of the ELAN, however, has been verified by dipole localization [54]. Abbreviations: BA, Brodmann's area; ELAN, early left-anterior negativity; ERP, event-related brain potential; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; MTG, middle temporal gyrus; MTL, middle temporal lobe; PET, positron imaging tomography; STG, superior temporal gyrus.

controlled) and/or different time windows during processing (early versus late). However, we are able to distinguish early from late processes using electrophysiological techniques that register the brain's reaction to a given item millisecond-by-millisecond from its onset.

I propose a neurocognitive model of sentence comprehension, the temporal parameters of which are based on electrophysiological data and neurotopographical specifications on brain-imaging data. The temporal characteristics of the model consist of three phases. Phase 1 (100–300 ms) represents the time window in which the initial syntactic structure is formed on the basis of information about the word category. During phase 2 (300–500 ms), lexical-semantic and morphosyntactic processes take place with the goal of thematic role assignment. During phase 3 (500–1000 ms), the different types of information are integrated. Although building of the syntactic-phrase structure is autonomous and precedes semantic processes in the early-time windows, these processes interact only in the late-time window. From this perspective, I argue that both psycholinguistic views, autonomous processing and interactive processing, hold in principle, but describe different processing phases during language comprehension (i.e. early versus late). The present model is, thus, compatible with both syntax-first models and interactive models that assume late interaction, but not with those that claim immediate or, even, predictive interaction. Although interaction between prosodic and syntactic information during auditory sentence comprehension is considered in the proposed model, the temporal structure of this interaction is not yet specified.

The functional neuroanatomy of auditory language comprehension is described as a bilateral temporo–frontal network in which the left temporal regions support processes that identify phonetic, lexical and structural elements; the left frontal cortex is involved with sequencing and the formation of structural, semantic and thematic relations; the right temporal region is thought to support the identification of prosodic parameters; and the right frontal cortex is involved in the processing of sentence melody. A schematic view of the processes that occur within the left hemisphere in this model is given in Fig. 1. This figure also sketches the role of working memory in the process of language comprehension (discussed briefly in Box 2). The model is based on empirical evidence from neurophysiological studies using event-related brain potentials (ERPs) and magnetic fields, and from imaging studies that include PET and fMRI. In this review, the neuroanatomy and the time course and

Box 2. The role of Broca's area in sentence comprehension

Broca's area has been anatomically defined to include BA 44 and BA 45 [a]. A classical view that Broca's area is the locus of syntax [b–d] is supported by brain-imaging studies showing that either BA 44 or BA 44/45 is active when comparing less complex subject-first sentences, such as 'The juice that the child spilled stained the rug.', with more complex object-first sentences, such as 'The child spilled the juice that stained the rug.' [e–g]. However, because the object noun 'juice' in the second sentence is not in its canonical position (subject–verb–object), these sentences differ not only in their complexity, but also in their working memory requirement. Aware of this, the authors claim that syntactic processes and the required memory recourses are responsible for the increase of activation in Broca's area.

A recent study in German varied the factor complexity (object first versus subject first) independently of the factor memory, that is the distance between the object-noun phrase and its original position in the structure (long versus short) [h]. Results using fMRI demonstrated that increased activation of Broca's area (BA 44) was triggered by the factor syntactic memory but not by complexity. This finding is compatible with the view that Broca's area is not the locus of syntax *per se* [i], but that it supports aspects of syntactic memory. Local phrase-structure building seems to recruit the inferior tip of BA 44 and the frontal operculum, in particular [j].

It should be noted that the description presented above concerns the role of Broca's area in language comprehension. There is no doubt that this area also supports language production [k,l]. Moreover, this area is involved in the processing of musical sequences [m], the perception of the rhythm of motion [n] and the imagery of motion [o]. A common feature of these tasks is that they involve an aspect of sequencing, which suggests that Broca's area supports the processing of sequences in both language and non-language domains.

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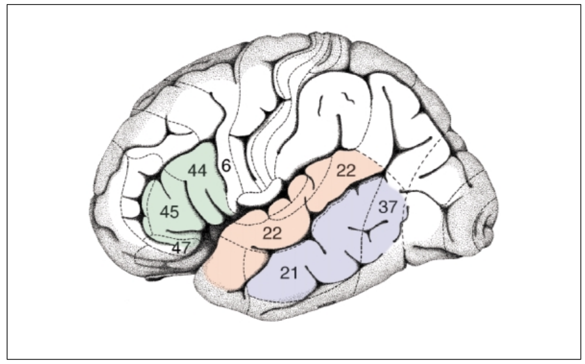

Fig. 2. Brodmann areas (BA) in the left hemisphere. The inferior frontal gyrus (IFG) is shown in green, the superior temporal gyrus (STG) in red and the middle temporal gyrus (MTG) in blue. (Adapted from Ref. [55].)

possible interplay of syntactic and semantic processes are specified. The neuroanatomy of prosodic processes and their interaction with syntactic processes are also discussed.

Syntactic and semantic processes

Neuroanatomy

The functional neuroanatomy of speech perception prior to syntactic and semantic processes has been described in detail recently by Hickok and Poeppel [8]. As the present review focuses on sentence-level processes, this processing stage is not considered here.

Studies on the functional neuroanatomy of semantic processes at the sentence level are rare. Rather, most imaging studies of semantic processes are conducted at the word level. Such studies indicate that the left middle temporal gyrus (MTG), the angular gyrus and the left inferior frontal gyrus (IFG) support semantic processes [9–12]. It is proposed that the frontal cortex is responsible for strategic and executive aspects of semantic processing [13–15]. Studies investigating semantic processes at the sentence level report a variety of activation loci, including the left IFG (Brodmann area, BA 45/47) [16], the right superior temporal gyrus (STG) and the left MTG [17], as well as the left posterior temporal region [18] (see Fig. 2). Studies that identified activation in temporal regions used a task in which subjects had to 'judge whether the sentence made sense'. Frontal activation of BA 45/47 was observed when subjects were asked to judge whether two sentences presented successively 'meant the same'. Although both tasks require an explicit judgment, the latter can only be performed after comparing the two sentences held in memory and, therefore, requires memory resources. Overall, the combined findings indicate that semantic processes are mainly subserved by the left temporal region and that the frontal cortex is recruited when strategic and/or memory aspects come into play.

Studies on the functional neuroanatomy of syntactic processes demonstrate involvement of the inferior frontal cortex and the anterior portion of

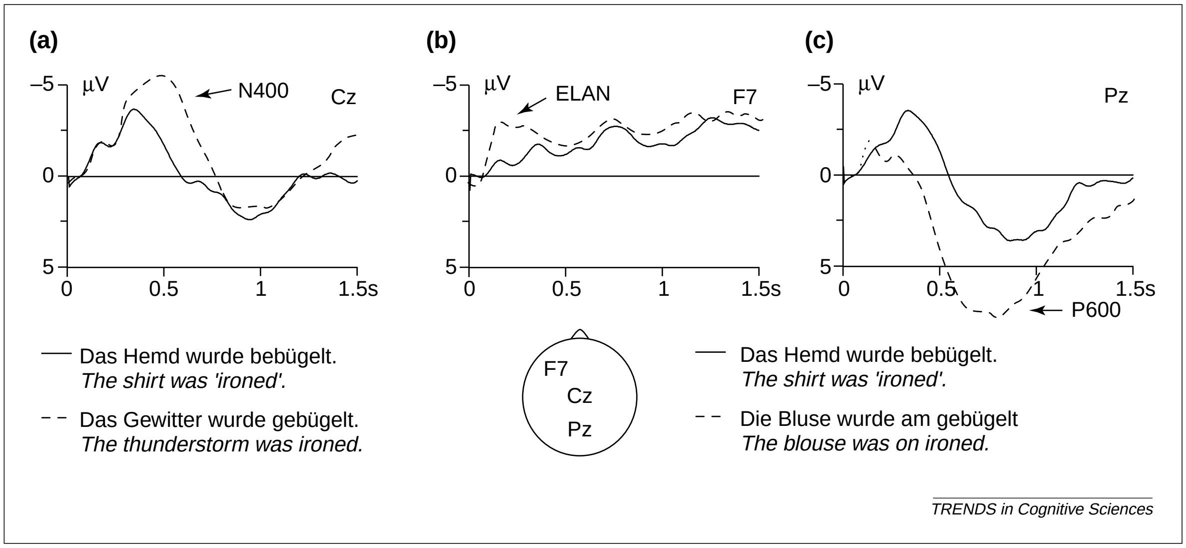

Fig. 3. The three language related components in the ERP: (a) N400, (b) very early left-anterior negativity (ELAN), and (c) P600. Shown are average ERPs for the semantic- and syntactic-violation condition at selected electrode sites. Solid lines represent the correct condition, and dotted lines the incorrect condition.

the temporal cortex. A consistent finding in studies that compare brain activation during simple and complex sentences (for details see Box 2) is that complex sentences are accompanied by increased activation of the left inferior frontal cortex (BA 44/45) [19–23]. These studies, however, use sentence materials in which the factor 'syntactic complexity' is confounded with the factor 'working memory'. A more recent study in which these two factors were varied independently demonstrates that activation of BA 44 is due to aspects of working memory rather than syntactic complexity [24].

Anterior and posterior temporal activation has been reported during sentence processing [16,18,22]. In particular, the anterior STG (planum polare) is active in a number of studies. This is accompanied by either substantial activation of the inferior frontal gyrus [16,18] or minimal or no activation in Broca's area, although activation in the left frontal operculum is sometimes observed [25–27]. Interestingly, the latter studies used auditory stimuli, which suggests that there is a partial difference in sentence comprehension between auditory and reading tests. It is probable that the involvement of the IFG during sentence reading occurs because of the process of phonological recoding during reading, a process that is attributed to the IFG on the basis of studies at the phoneme- and word level [9,28–30].

Thus, the combined neuroimaging data indicates that both semantic and syntactic processes involve parts of the temporal and the inferior frontal cortex. The left MTG and BA 45/47 are the relevant areas in the semantic domain, although activation of BA 45/47 appears to depend on the amount of strategic and/or memory processes required. In the syntactic domain, the relevant temporal region is the anterior left STG and the relevant frontal regions are left BA 44 and the adjacent frontal operculum. Although a larger portion of BA 44 seems to support aspects of syntactic working memory, the inferior tip of BA 44 and the frontal operculum are required specifically for local phrase-structure building.

Time course

Although many studies have investigated the time course of syntactic and semantic processes, only a few have investigated their direct interplay. The electrophysiological outcome of semantic processes is a negative wave, the so-called N400, that peaks about 400 ms after the word onset [31] and occurs in response to words that cannot be integrated semantically into the preceding context [32]. Syntactic processes are correlated with two ERP components, a left-anterior negativity (LAN), which occurs during an early time window (between 100–500 ms) and a late centro-parietal positivity, termed P600, which occurs between 600–1000 ms. Within the early time window, a very Early LAN (ELAN) correlates with rapidly detectable word-category errors [33–36] whereas the LAN correlates with morphosyntactic errors [37–40]. The P600 correlates with outright syntactic violations (following the ELAN), with 'garden-path' sentences that require syntactic revision, and with processing of syntactically complex sentences [41–44]. The three different ERP components and example sentences are displayed in Fig. 3.

The electrophysiological data clearly support the three-phase neurocognitive model presented at the start of this review. However, additional evidence is needed before the claims about modular syntactic processes during the early-time window (phase 1) and interactivity between semantic and syntactic processes during the late-time window (phase 3) can be justified. This evidence is provided by experiments in which the critical word in the sentence violates both the syntactic and semantic constraints set by the prior context, thus leading to

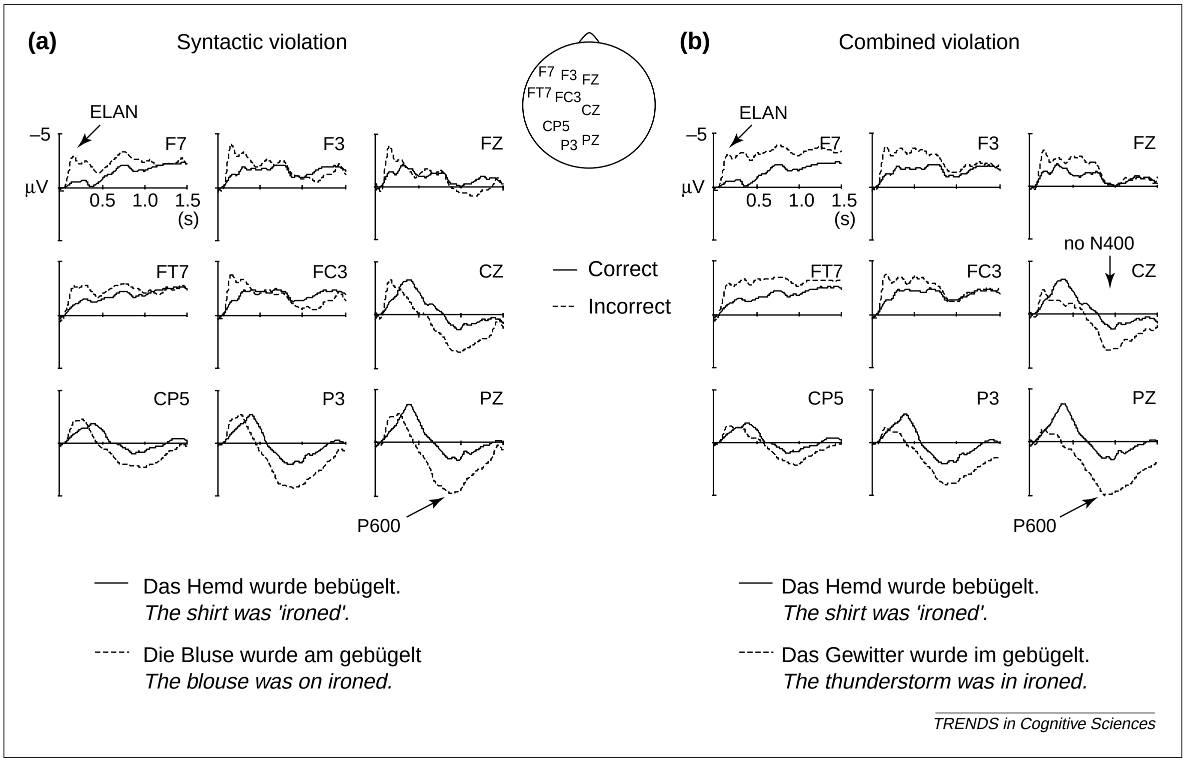

Fig. 4. Average ERPs for the syntactic violation (a) and the combined violation (b). Solid lines represent the correct condition, and dotted lines the incorrect condition. (Adapted from Ref. [47].)

difficulties in both processing domains. When a word-category violation, usually reflected by the ELAN (phase 1), and a semantic violation, usually reflected by the N400 (phase 2), are combined in one target word, only an ELAN is observed [45,46] (see Fig. 4). The absence of an N400 in double-violation conditions possibly occur because a target word that is not licensed by the syntax is not lexically integrated. This finding indicates that syntactic-structure building precedes semantic processes. When combining a morphosyntactic violation (e.g. syntactic gender) usually reflected by the LAN (phase 2) and a semantic anomaly usually reflected by the N400 (phase 2), both ERP components are present and independent of one another. In this condition, the amplitude of the P600 varies as a function of both the semantic and syntactic factors, thus suggesting an interaction between these factors in the late-time window (phase 3) [39].

There are some reports of experiments using ERPs that do not show ELAN effects in response to syntactic violations. We have demonstrated [47,48] that most of these studies used sentence material that did not contain outright syntactic violations, rather they contained correct, although unusual, structures. The finding that correct but unusual structures evoke only a P600, and not an ELAN, is expected on the basis of the present model and suggests that the brain reacts in accordance with the grammar.

In summary, different subparts of the left temporal- and frontal cortices subserve semantic and syntactic processing. Processes of identification (word category and meaning) that are assumed to be encoded in the mental lexicon might be located primarily in temporal structures, and the construction of syntactic relations (structure building) and semantic relations (categorization and selectional restriction) appear to involve the frontal cortex. Sentence comprehension consists of three functionally distinct phases: an initial parsing phase (phase 1), which precedes processes of thematic assignment based on semantic and morphosyntactic information (phase 2), and a late phase of revision during which interaction between semantic and syntactic information might take place (phase 3).

So far I have discussed the processing of semantic and syntactic information contained in sentences presented visually and auditorily. However, prosodic information encoded in the auditory presentation mode is an additional, relevant parameter.

Prosodic processes

The functional neuroanatomy of prosodic processes has been specified in recent studies using PET and fMRI. At the segmental level, pitch discrimination in speech syllables correlates with an increased activation in the right prefrontal cortex [49]. Violations of pitch for lexical elements in a tonal language, such as Thai, results in modulation of activation in the left frontal operculum adjacent to Broca's area [50]. Processes at the suprasegmental level, in which pitch modulations act as syntactic markers appear, instead, to involve the right hemisphere. A recent

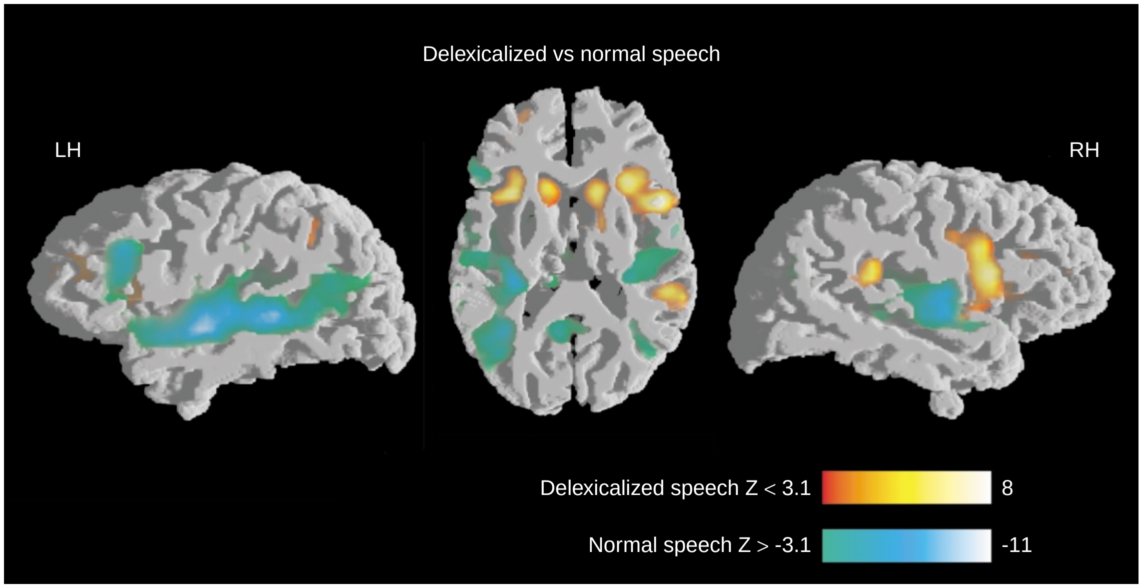

Fig. 5. Aspects of prosodic processing apparent from functional magnetic resonance imaging data. Functional brain activation in different subjects was averaged and superimposed onto a white-matter segmented, normalized anatomical volume. Comparing normal speech with delexicalized speech (filtered normal sentence that leaves the F_O contour intact but filters out all lexical information) reveals that left perisylvian areas are strongly involved in processing grammatical information whereas right perisylvian areas subserve the processing of slow prosodic modulations in spoken sentences.

fMRI experiment that systematically varied the presence of pitch information (normal intonation versus synthesized, flattened intonation) and of syntactic information (normal speech versus synthesized, delexicalized speech) at the sentential level identified modulations in activity of the right peri-sylvian cortex. In particular, the right superior temporal region and the fronto-opercular cortex were identified as regions that support the processing of suprasegmental information [51] (see Fig. 5).

Although the available neuroanatomical data are suggestive, the temporal structure of the processing of prosodic information with respect to other information types is still an empirical issue. There is electrophysiological evidence that prosodic information interacts with syntactic information at some point [52], although the time course of this interaction is not yet specified. This evidence stems from an ERP experiment conducted in German, in which syntactic and prosodic phrasing either did or did not match [52]. In the prosodic-mismatch condition, a prosodic-phrase boundary (which indicates a transitive-verb structure) present two words before a transitive verb caused problems for listeners in integrating the verb into the prior context. These problems were evidenced in a biphasic N400–P600 pattern, reflecting the difficulty of lexical-semantic integration (N400) and the possible attempt to revise the initial structure (P600) built on the available syntactic and prosodic information. These ERP findings indicate that both types of information interact but that they are mute with respect to the temporal structure because the measure was taken words after the misguiding prosodic information. Overall, although limited, the data available indicate that a temporo–frontal network that is predominantly within the right hemisphere supports prosodic processes and that prosodic information can influence syntactic processes.

Conclusion

In summary, I have argued that a bilateral temporo–frontal network subserves auditory-sentence comprehension. Although syntactic and semantic information are processed predominately by the left hemisphere, processing of prosodic information occurs predominantly in the right hemisphere. Temporal regions support identification processes, with syntactic processes involving the left anterior STG, semantic processes recruiting the left MTG and prosodic processes involving the right posterior STG. Frontal regions, by contrast, support the formation of relationships, with syntactic relationships involving BA 44 and the frontal opercular cortex, and semantic relationships recruiting BA 45/47. These different areas within the network must be activated and coordinated to achieve auditory sentence comprehension. The timing of the syntactic processes of structure building precedes, and are initially independent of, semantic processes, although both interact during a later processing phase. Prosodic processes influence syntactic processes, however, the exact timing of this is a subject for future research.

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