The cortical language circuit: from auditory perception to sentence comprehension

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Over the years, a large body of work on the brain basis of language comprehension has accumulated, paving the way for the formulation of a comprehensive model. The model proposed here describes the functional neuroanatomy of the different processing steps from auditory perception to comprehension as located in different gray matter brain regions. It also specifies the information flow between these regions, taking into account white matter fiber tract connections. Bottom-up, input-driven processes proceeding from the auditory cortex to the anterior superior temporal cortex and from there to the prefrontal cortex, as well as top-down, controlled and predictive processes from the prefrontal cortex back to the temporal cortex are proposed to constitute the cortical language circuit.

A model of the brain basis of language comprehension

The human ability to process language has been of scientific interest for more than a thousand years. However, it is only with the advent of neuroimaging techniques that our knowledge concerning the neural basis of different aspects of language processing has dramatically increased. A number of recent reviews have gathered together this knowledge, providing informative overviews [1–5].

The data now available provide a first opportunity to describe the entire processing stream from auditory perception to sentence comprehension and its neural basis. Specifically, functional activations observed in language-relevant brain regions, as well as the functional and structural connectivity between these regions, provide a good basis for the formulation of a coherent functional neuroanatomical model of language comprehension.

The proposed model displayed in Figure 1 is based on the currently available evidence about the specific language functions of particular cortical regions, as well as the structural connections between them, and attempts to describe the information flow within this network. The model will be subject to modification as new data become available and must be viewed as an opinion on the basis of which hypotheses for future research can be formulated.

Dorsal and ventral language pathways

Early patient studies [6,7] established that the brain regions relevant for language are located in the inferior frontal and temporal cortices with dominance in the left hemisphere. The standard view holds that these cortices are connected via ventral and dorsal pathways [3,8–10], with the ventral pathway subserving auditory-to-meaning mapping and the dorsal pathway supporting auditory-to-motor mapping [8,9]. However, there is recent evidence to suggest that the dorsal pathway is also involved in syntactic processing, in particular when sentences are complex [11–13]. Given the dissimilarity of these two functions allocated to the dorsal pathway, it has been proposed that there are two dorsal streams that can be separated functionally and structurally, at least with respect to their end points [5,14]. One pathway connects the temporal cortex to the premotor cortex (PMC) via the inferior parietal cortex (IFC) and parts of the superior longitudinal fasciculus (SLF); the other pathway connects the temporal cortex to Brodmann Area (BA) 44 as part of Broca's area via the arcuate fasciculus (AF).

The ventral pathway also seems to be responsible for more than one function: it is assumed to support sound-to-meaning mapping [9,11], as well as local syntactic structure building [12] or syntactic processes in general [15]. The ventral pathway consists of two fiber tracts that run closely together: the uncinate fasciculus (UF), which connects the anterior ventral inferior frontal cortex to the temporal pole, and the extreme capsule fiber system (ECFS), which mediates the inferior fronto-occipital fasciculus (IFOF), connecting the inferior frontal cortex along the temporal cortex to the occipital cortex. Within the temporal cortex, the inferior and middle longitudinal fasciculi provide a connection between its anterior and posterior regions. The particular functions these fiber tracts have during language processing are still a matter of debate [15–17]. The present model assumes two functionally and (partly) structurally different dorsal pathways, and considers two ventral pathways in their possible relevance for semantic and syntactic processing during language comprehension. With these four structural pathways and functional data as priors, I will draw a blueprint of the dynamic process from auditory input to sentence comprehension.

The temporal cortex: from auditory perception to words and phrases

Auditory perception is the initial stage in the auditory language comprehension process. The acoustic-phonological analysis and the processing of phonemes are performed

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  http://dx.doi.org/10.1016/j.tics.2012.04.001 Trends in Cognitive Sciences, May 2012, Vol. 16, No. 5

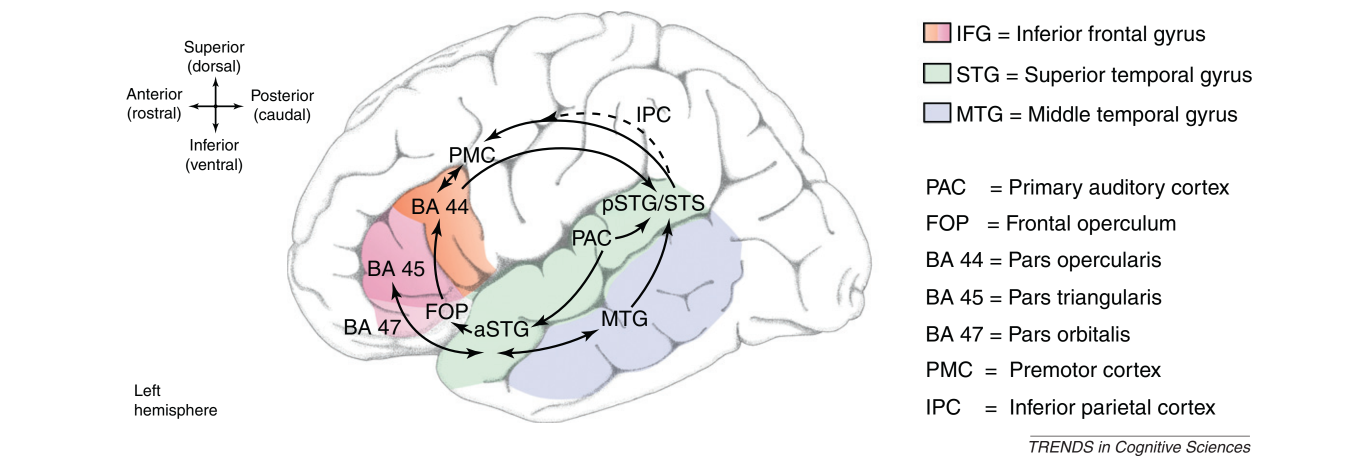

Figure 1. The cortical language circuit (schematic view of the left hemisphere). The major gyri involved in language processing are colorcoded. In the frontal cortex, four language-related regions are labeled: three cytoarchitectonically defined Brodmann [39] areas (BA 47, 45, 44), the premotor cortex (PMC) and the ventrally located frontal operculum (FOP). In the temporal and parietal cortex the following regions are labeled: the primary auditory cortex (PAC), the anterior (a) and posterior (p) portions of the superior temporal gyrus (STG) and sulcus (STS), the middle temporal gyrus (MTG) and the inferior parietal cortex (IPC). The solid black lines schematically indicate the direct pathways between these regions. The broken black line indicates an indirect connection between the pSTG/STS and the PMC mediated by the IPC. The arrows indicate the assumed major direction of the information flow between these regions. During auditory sentence comprehension, information flow starts from PAC and proceeds from there to the anterior STG and via ventral connections to the frontal cortex. Back-projections from BA 45 to anterior STG and MTG via ventral connections are assumed to support top-down processes in the semantic domain, and the dorsal back-projection from BA 44 to posterior STG/STS to subserve top-down processes relevant for the assignment of grammatical relations. The dorsal pathway from PAC via pSTG/STS to the PMC is assumed to support auditory-to-motor mapping. Furthermore, within the temporal cortex, anterior and posterior regions are connected via the inferior and middle longitudinal fasciculi, branches of which may allow information flow from and to the mid-MTG.

in the left middle portion of the superior temporal gyrus (STG) [18,19], lateral to Heschl's gyrus, which houses the primary auditory cortex (PAC). The processing of auditorily presented words is located in a region anterior to Heschl's gyrus in the left STG. This region has been considered as the area where the processing of auditory word forms (i.e., a word's phonological form) takes place [20–22]. Neurophysiological evidence suggests that the recognition of a word form's lexical status (word vs. pseudoword) is ultra-rapid (50–80 ms) [23] and so is the initial response to a word syntactic category error (40–90 ms) [24], which may be due to the recognition of a particular morphological word form. MEG source analyses reported that the very early word recognition effect is supported by left perisylvian sources and the right temporal lobe [23]. The early word category effect was registered in the anterior STG (aSTG) bilaterally [24].

Once the phonological word form is identified, its syntactic information and semantic information must be retrieved in a subsequent step. Words belong to particular word classes and categories. The information about a word's syntactic category allows the initial construction of syntactic phases. Based on neurophysiological data, these phrase structure building processes have been localized in the anterior superior temporal cortex approximately 120–150 ms after word category information is available as an early automatic syntactic process [24–26]. The involvement of the aSTG during syntactic phrase structure building has been confirmed by functional MRI (fMRI) studies using syntactic violation paradigms [27], as well as a natural language listening paradigm [28]. It has been proposed that, in the adult brain, these processes can be fast because templates of different phrase structures (e.g., determiner phrase, prepositional phrase) represented in the aSTG/STS are available automatically once the phrasal head (e.g. determiner, preposition) is encountered [29]. The observed anterior-running gradient from PAC to aSTG/STS moving from phonemes to words and phrases finds support in a recent meta-analysis [22].

The processing of semantic information is covered in a wide range of literature, mostly with a focus on semantic memory investigated at the word or item level [30]. Here, I will discuss lexical-semantic access and integration as it is necessary for sentence comprehension. Electrophysiology provides an interesting entry to this topic as a particular event-related potential (ERP) component reflecting lexical-semantic processes at the word and sentence level has been identified. Lexical-semantic access occurs fast, that is, approximately 110–170 ms after the word recognition point, whereas the well-known N400 effect (350–400 ms) is assumed to reflect controlled processes [23,31,32]. In sentential context, these lexical-semantic context effects, elicited by low cloze probability compared to high cloze probability words, are usually reported between 350 and 400 ms, starting at 200 ms [33]. In fMRI studies, lexical-semantic processes have mainly been observed in the middle temporal gyrus (MTG), although they do not seem to be confined to this region: they also include the association cortices in the left and right hemisphere [34]. Semantic processes at the sentential level are more difficult to localize. They seem to involve the anterior temporal lobe, as well as the posterior temporal cortex and angular gyrus [35,36]. The particular function of the anterior and posterior brain regions in semantic processes is still a matter of debate [30].

Since the anterior temporal lobe appears to be involved in processing syntactic information and semantic information at least at the sentential level, the function of this neuroanatomical region has been discussed as reflecting general combinatorial processes which are involved in phrase structure building as well as in semantic combinatorics [9,11]. Humphries *et al.* [37], however, have argued for a partial separation of the two domains within the anterior temporal cortex, with the most anterior portion of the STS responding to syntactic manipulations and a region directly posterior to it reflecting the interaction of syntactic and semantic factors.

The posterior regions (posterior STG/STS and angular gyrus) seem instead to be activated as a function of a word's predictability in sentential context. Activation of the angular gyrus is reported when predictability of a word given the prior sentence context is high [36,38], whereas the posterior STG/STS is activated when expectancy between a verb and its direct object–argument is low [38]. So far it is not entirely clear how these results can be integrated. It becomes clear, however, that the angular gyrus activation and the posterior STG/STS activation are part of different functional networks. Although posterior STG/STS is often reported to covary with BA 44 [38,39] and the right posterior STS, the angular gyrus often covaries with the left lateral and medial superior frontal gyri and the ventral IFG (BA 47) [36,40]. Functionally, this could mean that general predictability [36] and expectancy of verb–argument relation do not engage the same network. The finding that verb–argument processing is related to activation in the posterior STG/STS is in line with earlier studies [27,41]. The literature, however, does not provide strong views as to whether the activation in these posterior regions is a result of information transfer within the temporal cortex, or a result of information also provided by the IFG.

Structurally, information transfer from the PAC to the anterior STG and the posterior STG is in principle provided by short-range fiber tracts within the superior temporal cortex. These tracts have been shown to be functionally relevant in auditory processing [42]. Information transfer from the IFG would be guaranteed by the dorsal pathway connecting the posterior portion of Broca's area and the posterior temporal cortex (for further discussion of this pathway see section 'From inferior frontal cortex back to temporal cortex').

From temporal to frontal cortex: towards higher-order computation

Both syntactic and semantic processes involve the inferior frontal cortex, which can be subdivided cyto- and receptoarchitectonically into different subparts [43,44]. Within the inferior frontal cortex, the frontal operculum (FOP) and pars opercularis (BA 44) appear to subserve syntactic processes, and the pars triangularis (BA 45) and pars orbitalis (BA 47) seem to support semantic processes. For further language processing, the information thus has to be transferred from the temporal cortex to the inferior frontal cortex where the next processing steps take place.

Concerning syntax, the system now has to deal with higher-order structural aspects in order to establish grammatical relations between the different phrases, which are delivered by the aSTG and FOP. In the case of sentences with a non-canonical surface structure (e.g., object-first sentences), reordering of phrasal arguments in the hierarchy must additionally be achieved. This process is supported by Broca's area in the IFG (for a review see [5] and the references therein). The studies on syntactic complexity reviewed in [5] indicated activation in BA 44 and in the posterior portion of BA 45. It appears that reordering of clearly marked phrases mainly involves the pars opercularis (BA 44), whereas the (re)computation of arguments that are moved from subordinate sentence parts recruit the posterior portion of BA 45 bordering BA 44.

As to sentential semantic aspects, the processing system now has to deal with the semantic and thematic fit between the different arguments (noun phrases) and the verb. Semantic aspects in general activate more anterior portions of the IFG, namely BA 47 and the anterior portion of BA 45, particularly when lexical processes are under strategic control [45,46] or when top-down in sentential semantic context are examined [4,36,45].

In order to achieve these higher-order syntactic and semantic processes in the IFG, the information on the basis of which these computations take place must be transferred from the temporal cortex to the inferior frontal cortex via structural connections. The information transfer from the anterior temporal cortex and prefrontal cortex is assumed to be supported mainly by the ventral fiber tracts [8,9,12,16,47,48]. Two ventral tracts connect the temporal and the frontal cortex: the UF, which connects the more medio-ventrally located FOP with the anterior temporal cortex and temporal pole, and the ECFS, which mediates the IFOF connecting the more laterally located BA 45 and BA 47 with the temporal and occipital cortex [47,48]. These two ventral pathways are not easily separable structurally as they both run closely together when passing the ECFS [17]. These ventral pathways providing the basis for this information transfer are not easily separable functionally due to the fact that they run closely together. Moreover, they are not easily separable based on patient studies due to the fact that ventral pathwaylesions are reported to cause semantic and syntactic comprehension deficits [49]. However, given that the target regions in the inferior frontal gyrus (IFG) have been functionally separated, with the more anterior region of the IFG assumed to support semantic processes and the more posterior region of the IFG suggested to subserve syntactic processes [5,50], a functional separation can be proposed.

Semantic information appears to be transferred from the temporal cortex to the anterior portion of the IFG via the ventral pathway through the ECFS to BA 47 and BA 45, as indicated indirectly by combined fMRI and diffusion weighted MRI (dMRI) studies and most directly by patient studies (for reviews see [8,48]). Syntactic information, however, seems to be transferred from the anterior STG/STS to the FOP also via a ventral connection as indicated by a combined fMRI/dMRI study [12], and from there to the posterior portion of the IFG, where higher-order syntactic computations take place [17,51,52]. Based on these findings, the temporo-frontal network of syntactic processing can be modeled to involve the anterior STG/STS and the posterior IFG mediated ventrally by the FOP. The system of semantic processing is assumed to involve the middle temporal gyrus (MTG), the anterior temporal lobe, and the anterior portion of the IFG.

It has been argued that during sentence processing semantic and syntactic information interact in the IFG in general [53,54], and especially for the purpose of argument hierarchization [29]. Hagoort [53] has called the entire region of the IFG spanning from BA 47 to BA 44 a unification space which enables integration. Interestingly, empirical findings suggest that interaction and integration of semantic and syntactic information recruit not only the IFG but also the posterior temporal cortex [55,56]. Other results argue in favor of the posterior temporal cortex as the dominant region of semantic/syntactic integration [5,45]: this region was seen to be activated in addition to BA 44 during processing syntactic structures in meaningful sentences [57], but not for similar structures in an artificial grammar [12], whereas BA 44 was activated in both studies. BA 44 is the core region of syntactic processes across different languages [5] and tasks [58], whereas the posterior temporal region comes into play when argument assignment in the service of sentence interpretation is required [9,41,45,55,56].

From inferior frontal cortex back to temporal cortex

In this article, I assume that the region of semantic/syntactic integration is located in the posterior temporal cortex [5,41,45]. This region must, therefore, receive input from BA 44 as the core syntax region [5,56] and from semantic regions [50], that is, either BA 45 or BA 47 [42,45], the angular gyrus [37,59] or the MTG [60].

During syntactic processing, the reported activations in BA 44 and the posterior temporal cortex in the comprehension of syntactically complex sentences [41,57] raise the question of how these regions are functionally related. It has been argued that BA 44 plays a particular role in creating argument hierarchies as a sentence is computed [29,51]. There is a long-standing debate concerning the issue of whether the processing of syntactically complex sentences requires support from working memory [61–64]. There is strong evidence that the most dorsal part of BA 44 and the adjacent inferior frontal sulcus support syntactic working memory when sentences are syntactically challenging [61,65] and, moreover, that these two regions within the inferior frontal cortex are connected functionally and structurally by short-range fiber tracts [65]. This frontally located syntactic working memory system appears to be distinguishable from the phonological working memory system located in the parietal cortex. Support for this view comes from a recent study that presented sentences in which the sheer distance between a given argument and its verb was varied in length, thereby increasing phonological working memory demands [66]. In this study, the main effect of distance was located parietally. This distance effect did not interact with the syntax factor (argument order), which in turn was located in BA 44 [66]. However, to achieve sentence comprehension, information exchange between the prefrontal cortex and the parietal cortex must take place. Here, I assume that the information flow between these regions is bidirectional. The necessary structural connection between these regions is provided by parts of the superior longitudinal fasciculus [66,67].

An additional function of the posterior IFG might be to deliver syntactic predictions about the incoming information in a sentence to the temporal cortex. Such predictions would not concern a particular word but rather a particular class of words. For example, once the parser has processed three arguments in a sentence, it expects the sentence-final verb to belong to a verb class that takes three arguments. The violation of such an expectation has been shown to result in a biphasic N400–P600 ERP pattern [68]. These predictions might be transferred top-down via the dorsal pathway connecting the posterior IFG (BA 44/45) to the posterior temporal integration cortex, through the SLF/AF [12,46] either via a direct connection or an indirect connection mediated by the parietal cortex [69].

A recent fMRI study indicates that sentence context may not enhance lower-level perceptual processes directly but that the comprehension system may instead delay bottom-up commitments until lower-level and higher-level representations can be combined [70]. ERP data suggest that top-down processes work in parallel with bottom-up processes. For the semantic sentential domain, it has been shown that, in the absence of complete phonetic information, word recognition relies both on top-down information delivered by the semantic context and bottom-up information provided by the remaining word fragment [71]. Thus, both of these studies suggest that, at least during sentence processing, top-down effects are located at the integration level rather than at the level of sensory perception.

The present model remains open with respect to how exactly semantic information is delivered to the posterior temporal cortex for integration. At least two processing streams are possible. First, if the assumption that the function of the anterior IFG is to mediate top-down controlled semantic retrieval of lexical representations located in the MTG [35] is valid, then semantic information could be transferred from BA 47/45 via the ventral pathway through the ECFS to the posterior temporal cortex [11], with additional information collected from the lexical-semantic system in the MTG [54] by the middle longitudinal fasciculus [11]. Second, it is also possible that semantic information processed in BA 47/45 and integrated with syntactic information from BA 44/45 in the IFG [53]. If this is the case, then it could be transferred from there via the SLF/AF to the angular gyrus and the posterior temporal cortex. Further research must determine which of these assumptions are valid.

Pathways and functions

The present model formulates functional claims concerning the structure of the dorsal and ventral pathways, and makes predictions about the direction of information flow for these pathways. First, it is claimed that there are two dorsal fiber tracts [5,69,72]: one connecting the temporal cortex with PMC and one connecting the temporal cortex with BA 44. The former connection supports sensory-to-motor mapping in a bottom-up manner [9,11] and is already present at birth [73]. The latter connection only develops as the brain matures [73,74] and is functionally related to the processing of syntactically complex sentences [75] and may deliver predictions to the posterior temporal cortex in a top-down manner. Evidence for a structural separation within the dorsal pathway has been provided by developmental studies [73,75]. Functionally, it has been demonstrated that children at an age when they still have problems with the processing of syntactically complex sentences do not show a fully matured fiber connection between BA 44 and the posterior temporal cortex [75]. Second, it is assumed that syntactic information is processed via both the ventral and the dorsal pathways: the ventral pathway supports syntactic phrase structure building and the dorsal pathway, with BA 44 involvement, supports the processing of syntactically complex sentences. Evidence for an involvement of both pathways during syntactic processing is evidenced by combined fMRI/dMRI studies [12,66] as well as by patient studies [13,15,76].

Dynamic causal modeling (DCM) of auditory sentence processing will be helpful in determining whether the assumed information flow is valid. To date, very few DCM studies on sentence processing are available. One DCM study used data from an auditory processing experiment which had identified four activation clusters for the processing of syntactically complex sentences: IFG (BA 45), premotor cortex, posterior STS and anterior MTG [77]. All models tested assumed bidirectional intrinsic connectivity between these four regions as mentioned. The prevailing model was the model with IFG as the input, where syntactic complexity modulated the flow of information from IFG to posterior STS, reflecting the importance of this connection for parsing complex syntactic sentences. Another DCM study analyzed data from a reading experiment varying the syntactic complexity of the sentences (Makuuchi, M. *et al.*, unpublished data). In this study four activation clusters were identified: BA 44 and the inferior frontal sulcus (IFS) in the IFG, the IPC and the posterior temporal cortex (TC). In all models, the four regions were modeled as bidirectional. As this was a reading study, the visual word form area in the fusiform gyrus (FG) was taken as the input. The different models varied in their connections from the FG. The prevailing model indicated bottom-up information flow from FG via the IPC (known as the phonological working memory system) to the IFS (known as the syntactic working memory system). From the IFG, information flows back to the posterior TC, as a direct functional connection from BA 44 and as an indirect connection from IFS mediated by the IPC. These studies provide the first evidence that information flows from the IFG back to the posterior temporal cortex, as assumed, via the dorsal pathway.

The ultimate description of information flow, however, should not be based on DCM only [78], as only strong priors allow realistic modeling. In the future, it will be necessary to work both on the physiological reality of those priors, as well as on the development of novel modeling approaches.

Concluding remarks

In conclusion, the language circuit modeled here must be conceptualized as a dynamic temporo-frontal network with initial input-driven information processed bottom-up from the auditory cortex to the frontal cortex along the ventral pathway, with semantic information reaching the anterior IFG, and syntactic information reaching the posterior IFG. The anterior IFG is assumed to mediate top-down controlled lexical-semantic access to the MTG and semantic predictions to the posterior temporal cortex via the ventral pathway. The posterior IFG is assumed to support hierarchization of phrases and arguments and to possibly mediate verb–argument related predictions via the dorsal pathway to the posterior temporal cortex where integration of syntactic and semantic information takes place. Box 1 provides a list of key questions for future research based on this model.

Box 1. Questions for future research

- Given that the present model only considers information flow in the left hemisphere, an extended model would need to incorporate the contributions of the right hemisphere and its interaction with the left hemisphere (as discussed in [5,8]).
- It is known that subcortical structures, i.e. the thalamus and basal ganglia, are involved in language processing. Their particular contribution to language processing and their functional and structural connectivity need to be evaluated.
- The interplay between function (electrical signalling) and structure (myelin formation) is known from animal *in vitro* studies [79] and human *in vivo* training studies [80]. Thus, the question arises to what extend particular fiber tracts are affected by aspects of language learning.
- The contribution of the syntactic working memory system (located in the prefrontal cortex) [65] and the phonological working memory system (located in the parietal cortex) [66] and their interaction during language processing needs to be described in a future model.
- The developmental change of the impact of bottom-up processes and top-down processes will need to be investigated, given that the latter processes can only come into play once linguistic knowledge is acquired.

Acknowledgements

I acknowledge three anonymous reviewers for their comments on an earlier version of the manuscript and Jonas Obleser for his most helpful feedback on the final version.

References

1 Friederici, A.D. (2002) Towards a neural basis of auditory sentence processing. *Trends Cogn. Sci.* 6, 78–84
2 Vigneau, M. *et al.* (2011) What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis. *Neuroimage* 54, 577–593
3 Rauschecker, J.P. and Scott, S.K. (2009) Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nat. Neurosci.* 12, 718–724
4 Price, C.J. (2010) The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann. N. Y. Acad. Sci.* 1191, 62–88
5 Friederici, A.D. (2011) The brain basis of language processing: from structure to function. *Physiol. Rev.* 91, 1357–1392
6 Broca, P. (1861) Remarques sur le siége de la faculté du langage articulé, suivies d'une observation d'aphémie (parte de la parole). *Bull. Soc. Anat. Paris* 6, 330–357
7 Wernicke, C. (1874) *Der aphasische Symptomencomplex*, Springer Verlag
8 Hickok, G. and Poeppel, D. (2004) Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition* 92, 97–99
9 Hickok, G. and Poeppel, D. (2007) The cortical organization of speech perception. *Nat. Rev. Neurosci.* 8, 393–402
10 Rauschecker, J.P. and Tian, B. (2000) Mechanisms and streams for processing of 'what' and 'where' in auditory cortex. *Proc. Natl. Acad. Sci. U.S.A.* 97, 11800–11806
11 Saur, D. *et al.* (2008) Ventral and dorsal pathways for language. *Proc. Natl. Acad. Sci. U.S.A.* 105, 18035–18040
12 Friederici, A.D. *et al.* (2006) The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proc. Natl. Acad. Sci. U.S.A.* 103, 2458–2463

13 Wilson, S.M. *et al.* (2010) Neural correlates of syntactic processing in the nonfluent variant of primary progressive aphasia. *J. Neurosci.* 30, 16845–16854
14 Friederici, A.D. (2012) Language development and the ontogeny of the dorsal pathway. *Front. Evol. Neurosci.* 4, http://dx.doi.org/10.3389/fnevo.2012.00003
15 Tyler, L.K. *et al.* (2011) Left inferior frontal cortex and syntax: function, structure and behaviour in patients with left hemisphere damage. *Brain* 134, 415–431
16 Friederici, A.D. (2009) Pathways to language: fiber tracts in the human brain. *Trends Cogn. Sci.* 13, 175–181
17 Weiller, C. *et al.* (2009) Please don't underestimate the ventral pathway in language. *Trends Cogn. Sci.* 13, 369–370
18 Obleser, J. *et al.* (2007) Multiple stages of auditory speech perception reflected in event-related fMRI. *Cereb. Cortex* 17, 2251–2257
19 Leaver, A.M. and Rauschecker, J. (2010) Cortical representation of natural complex sounds: effects of acoustic features and auditory object category. *J. Neurosci.* 30, 7604–7612
20 Binder, J.R. *et al.* (2000) Human temporal lobe activation by speech and nonspeech sounds. *Cereb. Cortex* 10, 512–528
21 Cohen, L. *et al.* (2004) Distinct unimodal and multimodal regions for word processing in the left temporal cortex. *Neuroimage* 23, 1256–1270
22 DeWitt, I. and Rauschecker, J. (2011) Phoneme and word recognition in the auditory ventral stream. *Proc. Natl. Acad. Sci. U.S.A.* 109, E505–E514
23 MacGregor, L.J. *et al.* (2012) Ultra-rapid access to words in the brain. *Nat. Commun.* 3, http://dx.doi.org/10.1038/ncomms1715
24 Herrmann, B. *et al.* (2011) Syntactic and auditory spatial processing in the human temporal cortex: An MEG study. *Neuroimage* 57, 624–633
25 Friederici, A.D. *et al.* (2000) Localization of early syntactic processes in frontal and temporal cortical areas: a magnetoencephalographic study. *Hum. Brain Mapp.* 11, 1–11
26 Shtyrov, Y. *et al.* (2003) Grammar processing outside the focus of attention: an MEG study. *J. Cogn. Neurosci.* 15, 1195–1206
27 Friederici, A.D. *et al.* (2003) The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cereb. Cortex* 13, 170–177
28 Brennan, J. *et al.* (2012) Syntactic structure building in the anterior temporal lobe during natural story listening. *Brain Lang.* 120, 163–173
29 Bornkessel, I. and Schlesewsky, M. (2006) The extended Argument Dependency Model: a neurocognitive approach to sentence comprehension across languages. *Psychol. Rev.* 113, 787–821
30 Patterson, K. *et al.* (2007) Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8, 976–987
31 Brown, C. and Hagoort, P. (1993) The processing nature of the n400 – evidence from masked priming. *J. Cogn. Neurosci.* 5, 34–44
32 Chwilla, D.J. *et al.* (1995) The N400 as a function of the level of processing. *Psychophysiology* 32, 274–285
33 Van den Brink, D. *et al.* (2001) Electrophysiological evidence for early contextual influences during spoken-word recognition: N200 versus N400 effects. *J. Cogn. Neurosci.* 13, 967–985
34 Binder, J.R. *et al.* (2009) Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796
35 Lau, E.F. *et al.* (2008) A cortical network for semantics: (de)constructing the N400. *Nat. Rev. Neurosci.* 9, 920–933
36 Obleser, J. *et al.* (2007) Functional integration across brain regions improves speech perception under adverse listening conditions. *J. Neurosci.* 27, 2283–2289
37 Humphries, C. *et al.* (2006) Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *J. Cogn. Neurosci.* 18, 665–679
38 Obleser, J. and Kotz, S.A. (2010) Expectancy constraints in degraded speech modulate the language comprehension network. *Cereb. Cortex* 20, 633–640
39 Brodmann, K. (1909) Beiträge zur histologischen Lokalisation der Grosshirnrinde: VI. Die Cortexgliederung des Menschen. *J. Psychol. Neurol.* 10, 231–246
40 Uddin, L.Q. *et al.* (2010) Dissociable connectivity within human angular gyrus and intraparietal sulcus: evidence from functional and structural connectivity. *Cereb. Cortex* 20, 2636–2646
41 Bornkessel, I. *et al.* (2005) Who did what to whom? The neural basis of argument hierarchies during language comprehension. *Neuroimage* 26, 221–233
42 Upadhyay, J. *et al.* (2008) Effective and structural connectivity in the human auditory cortex. *J. Neurosci.* 28, 3341–3349
43 Amunts, K. *et al.* (1999) Broca's region revisited: cytoarchitecture and intersubject variability. *J. Comp. Neurol.* 412, 319–341
44 Amunts, K. *et al.* (2010) Broca's region: novel organizational principles and multiple receptor mapping. *PLoS Biol.* 8, e1000489
45 Newman, S.D. *et al.* (2010) The effect of semantic relatedness on syntactic analysis: an fMRI study. *Brain Lang.* 113, 51–58
46 Rodd, J.M. *et al.* (2005) The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cereb. Cortex* 15, 1261–1269
47 Anwander, A. *et al.* (2007) Connectivity-based parcellation of Broca's area. *Cereb. Cortex* 17, 816–825
48 Weiller, C. *et al.* (2011) How the ventral pathway got lost: and what its recovery might mean. *Brain Lang.* 118, 29–39
49 Tyler, L.K. *et al.* (2011) Left inferior frontal cortex and syntax: function, structure and behaviour in left-hemisphere damaged patients. *Brain* 134, 415–431
50 Vigneau, M. *et al.* (2006) Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *Neuroimage* 30, 1414–1432
51 Friederici, A.D. *et al.* (2006) Processing linguistic complexity and grammaticality in the left frontal cortex. *Cereb. Cortex* 16, 1709–1717
52 Grodzinsky, Y. (2000) The neurology of syntax: language use without Broca's area. *Behav. Brain Sci.* 23, 1–71
53 Hagoort, P. (2005) On Broca, brain, and binding: a new framework. *Trends Cogn. Sci.* 9, 416–423
54 Tyler, L.K. and Marslen-Wilson, W. (2008) Fronto-temporal brain systems supporting spoken language comprehension. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 363, 1037–1054
55 Snijders, T.M. *et al.* (2009) Retrieval and unification of syntactic structure in sentence comprehension: an fMRI study using word-category ambiguity. *Cereb. Cortex* 19, 1493–1503
56 Kuperberg, G.R. *et al.* (2000) Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: an fMRI study. *J. Cogn. Neurosci.* 12, 321–341
57 Friederici, A.D. *et al.* (2009) The role of the posterior superior temporal cortex in sentence comprehension. *Neuroreport* 20, 563–568
58 Caplan, D. *et al.* (2008) Task-dependent and task-independent neurovascular responses to syntactic processing. *Cortex* 44, 257–275
59 Humphries, C. *et al.* (2007) Time course of semantic processes during sentence comprehension. *Neuroimage* 36, 924–932
60 Vandenberghe, R. *et al.* (2002) The response of left temporal cortex to sentences. *J. Cogn. Neurosci.* 14, 550–560
61 Caplan, D. and Waters, G.S. (1999) Verbal working memory and sentence comprehension. *Behav. Brain Sci.* 22, 77–94
62 Fiebach, C.J. *et al.* (2005) Revisiting the role of Broca's area in sentence processing: syntactic integration versus syntactic working memory. *Hum. Brain Mapp.* 24, 79–91
63 Rogalsky, C. *et al.* (2008) Broca's area, sentence comprehension, and working memory: an fMRI Study. *Front. Hum. Neurosci.* 2, 14
64 Santi, A. and Grodzinsky, Y. (2010) FMRI adaptation dissociates syntactic complexity dimensions. *Neuroimage* 51, 1285–1293
65 Makuuchi, M. *et al.* (2009) Segregating the core computational faculty of human language from working memory. *Proc. Natl. Acad. Sci. U.S.A.* 106, 8362–8367
66 Meyer, L. *et al.* (in press) Linking ordering in Broca's area to storage in left temporo-parietal regions: the case of sentence processing. *Neuroimage*
67 Makris, N. *et al.* (2005) Segmentation of subcomponents within the superior longitudinal fascicle in humans: A quantitative, in vivo, DT-MRI study. *Cereb. Cortex* 15, 854–969
68 Friederici, A.D. and Frisch, S. (2000) Verb-argument structure processing: the role of verb-specific and argument-specific information. *J. Memory Lang.* 43, 476–507
69 Catani, M. *et al.* (2005) Perisylvian language networks of the human brain. *Ann. Neurol.* 57, 8–16
70 Sivonen, P. *et al.* (2006) Semantic retrieval of spoken words with an obliterated initial phoneme in a sentence context. *Neurosci. Lett.* 408, 220–225

71 Davis, M.H. *et al.* (2011) Does semantic context benefit speech understanding through 'top-down' processes? Evidence from time-resolved sparse fMRI. *J. Cogn. Neurosci.* 23, 3914–3932
72 Friederici, A.D. (2012) Language development and the ontogeny of the dorsal pathway. *Front. Evol. Neurosci.* 4, http://dx.doi.org/10.3389/fnevo.2012.00003
73 Perani, D. *et al.* (2011) The neural language networks at birth. *Proc. Natl. Acad. Sci. U.S.A.* 108, 16056–16061
74 Pujol, J. *et al.* (2006) Myelination of language-related areas in the developing brain. *Neurology* 66, 339–343
75 Brauer, J. *et al.* (2011) Neuroanatomical prerequisites for language functions in the maturing brain. *Cereb. Cortex* 21, 459–466
76 Griffiths, T.D. *et al.* (2012) Functional organization of the neural language system: dorsal and ventral pathways are critical for syntax. *Cereb. Cortex* http://dx.doi.org/10.1093/cercor/bhr386
77 den Ouden, D.B. *et al.* (2012) Network modulation during complex syntactic processing. *Neuroimage* 59, 815–823
78 Lohmann, G. *et al.* (2012) Critical comments on dynamic causal modeling. *Neuroimage* 59, 2322–2329
79 Wake, H. *et al.* (2011) Control of local protein synthesis and initial events in myelination by action potentials. *Science* 333, 1647–1651
80 Scholz, J. *et al.* (2009) Training induces changes in white-matter architecture. *Nat. Neurosci.* 12, 1370–1371