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This is a contribution from *Developmental Perspectives in Written Language and Literacy. In honor of Ludo Verhoeven.*

Edited by Eliane Segers & Paul van den Broek.

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The neural basis for primary and acquired language skills

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Reading is a cultural invention that needs to recruit cortical infrastructure that was not designed for it (cultural recycling of cortical maps). In the case of reading both visual cortex and networks for speech processing are recruited. Here I discuss current views on the neurobiological underpinnings of spoken language that deviate in a number of ways from the classical Wernicke-Lichtheim-Geschwind model. More areas than Broca's and Wernicke's region are involved in language. Moreover, a division along the axis of language production and language comprehension does not seem to be warranted. Instead, for central aspects of language processing neural infrastructure is shared between production and comprehension. Arguments are presented in favor of a dynamic network view, in which the functionality of a region is co-determined by the network of regions in which it is embedded at particular moments in time. Finally, core regions of language processing need to interact with other networks (e.g. the attentional networks and the ToM network) to establish full functionality of language and communication. The consequences of this architecture for reading are discussed.

Keywords: neurobiology of language, memory, unification, spoken language network, reading

1. Introduction

Our capacity for language is deeply rooted in our biological make-up. We all share the capacity to acquire language within the first few years of life, without any formalized teaching programme. Despite its complexity we master our native language well before we can lace our shoes or perform simple calculations. This is all based on the universal availability of a language-ready brain. At the same time, in modern society we have to acquire culturally determined language skills, such as reading and writing. These functions are not part of the language-ready brain. In the case of

reading, the required skills need to develop by the interaction between possibilities that the visual cortex provides and the neurobiological infrastructure for spoken language. As a result of formal training in reading, part of visual cortex develops a relative specialisation in recognizing visual word forms. In addition, functional connections need to develop with areas in temporal cortex that subserve phonological processing. In the remainder, we will focus especially on the biologically primary language system, that is the one for listening and speaking.

There is wide agreement that the architecture of our language system sets us apart from other species and is uniquely human. It is characterized by a tripartite architecture (Jackendoff, 2002) that enables us to map sound onto meaning (in listening) or meaning onto sound (in speaking). Next to sound and meaning, there is syntax, which enables the well-formed grouping of words into longer utterances. At a very general level, for all three information types (sound, syntax, meaning), one can make a distinction between two crucial components. The one relates to the common assumption that the basic building blocks of linguistic knowledge get encoded and consolidated in the course of language acquisition. This is what I hence refer to as the *Memory* component of the human language system, and is more usually called the mental lexicon in the field of psycholinguistics. When acquiring single word reading, a connection needs to be established between (components of) the visual word forms and information in this Memory component. Crucially, however, language processing is more than the retrieval of lexical knowledge and goes beyond the simple concatenation of retrieved lexical items. The expressive power of human language derives from the possibility to combine elements from memory in often novel ways. I have called this process of deriving new and complex meaning from the lexical building blocks *Unification* (Hagoort, 2005, 2013). Unification thus refers to the on-line assembly of lexical building blocks into larger structures, with contributions from context and general world knowledge. It instantiates what in linguistic theories is often called the compositionality of language. There is reason to believe that the compositional machinery of language is largely shared between speaking/listening and reading. The cognitive infrastructure of Memory and Unification is supported by the neurobiological infrastructure of the human brain to which I now turn.

2. The neurobiology of language

For more than a century the neurobiological model that has dominated the field was the Wernicke-Lichtheim-Geschwind (WLG) model (see Figure 1; Levelt, 2013). In this model, the human language faculty was situated in the left perisylvian cortex, with a strict division of labor between the frontal and temporal regions. Wernicke's

area in left temporal cortex was assumed to subserve the comprehension of speech, whereas Broca's area in left inferior frontal cortex was claimed to subserve language production. The arcuate fasciculus connected these two areas.

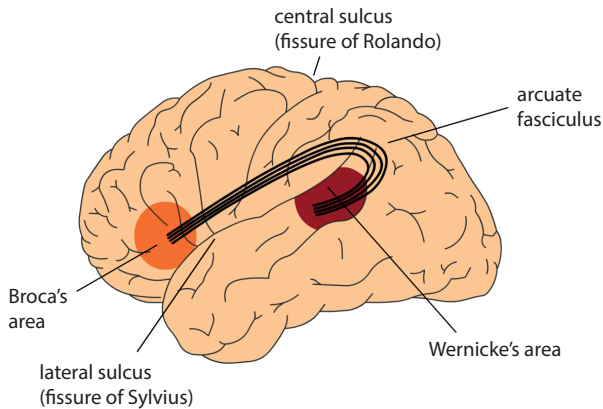


Figure 1. The classical Wernicke-Lichtheim-Geschwind model of the neurobiology of language. In this model Broca's area is crucial for language production, Wernicke's area subserves language comprehension, and the necessary information exchange between these areas (such as in reading aloud) is done via the arcuate fasciculus, a major fibre bundle connecting the language areas in temporal cortex (Wernicke's area) and frontal cortex (Broca's area). The language areas are bordering one of the major fissures in the brain, the so-called Sylvian fissure. Collectively, this part of the brain is referred to as perisylvian cortex

Despite its impact until this very day, the classical model is not a fully adequate account of the neurobiology of language. Although Broca's area, Wernicke's area and adjacent cortex are core nodes in the language network, the distribution of labor between these regions is different than was claimed in the WLG model. Lesions in Broca's region are known to impair not only language production but also language comprehension (Caramazza & Zurif, 1976), whereas lesions in Wernicke's region also affect language production. More recently, functional neuroimaging studies provided further evidence that the classical view on the role of these regions is no longer tenable. For example, central aspects of language production and comprehension are subserved by shared neural circuitry (Menenti et al., 2011; Segaert et al., 2012). Moreover, the classical model focused on single word processing, whereas a complete neurobiological account of language processing should also take into account what goes on beyond production and comprehension of single words. As a consequence of the mounting evidence against the classical WLG model, in recent years alternative neurobiological models for language have been proposed (e.g., Friederici, 2002, 2012; Hagoort, 2005, 2013; Hickock & Poeppel, 2007; Poeppel, this issue; Pulvermüller, 2013).

I here describe a very general model that I developed, and that has also been a source of inspiration for accounts of reading and dyslexia (e.g., see the dissertation of Margje van der Schuit, 2011; Blomert, 2011). I refer here to the Memory, Unification, and Control (MUC) model (Hagoort, 2005, 2013), in which the distribution of labor between Broca's area, Wernicke's area and adjacent cortical regions is as follows: Regions in the temporal cortex and in the inferior parietal cortex (angular gyrus, supramarginal gyrus) subserve the knowledge representations that have been laid down in memory during the acquisition of spoken language. These regions store information including phonological word forms, morphological information, and the syntactic templates associated with noun, verbs, adjectives (for details, see Hagoort, 2003, 2005, 2009). They also include semantic convergence zones, but on the whole conceptual knowledge is quite widely distributed (Binder & Desai, 2011). Dependent on knowledge type, different parts of temporal and parietal cortex are involved. Frontal regions (Broca's area and adjacent cortex) are crucial for unification operations. These operations generate larger structures from the building blocks that are retrieved from memory. Within left inferior frontal cortex (Unification Space), a spatial activation gradient is observed. The distribution of the activations seems to depend on the type of information that gets unified. Semantic unification recruits Brodmann's Area (BA) 47 and BA 45; syntactic unification has its focus in BA 45 and BA 44 (Hagoort & Indefrey, 2014), while phonological processes recruit BA 44 and ventral parts of BA 6. In addition, executive control needs to be exerted, such that the correct target language is selected, turn taking in conversation is orchestrated, the correct register is selected, attention is paid to the most relevant information in the input, and so forth. Control regions involve dorsolateral prefrontal cortex, and midline structures including the anterior cingulate cortex (ACC) and the parts of parietal cortex that are involved in attention (Duncan, 2010).

The picture that I sketched is largely based on fMRI data on language processing that were acquired in the last two decades (Price, 2010). However, one limitation of fMRI and lesion based analyses is that it results in a much more static picture than is warranted by the highly dynamic organization of neural events that unfold in the language network. Such a picture favors accounts in which brain areas have fixed contributions independent of time and context. However, this static view is incorrect. Language functions do not reside in single brain regions. Instead, language is subserved by dynamic networks of brain regions, including the ones just outlined. Ultimately, the mapping of a given language function onto the neural architecture of the brain appears to be in terms of a network of brain regions instantiating that particular language function (Fedorenko & Thompson-Schill, 2014; Mesulam, 1998; McIntosh, 2008; Sporns, 2011; Turken & Dronkers, 2011). Typically, each node in such a network will participate dynamically in other functional networks

as well. This view does not deny that a specific region (e.g., part of Broca's area) has an identifiable role, but it is crucial to understand that the execution of this role depends on the interaction with other regions that are part of the relevant network (Johansen-Berg, 2013). In short, "the mapping between neurons and cognition relies less on what individual nodes can do and more on the topology of their connectivity." (Sporns, 2011, p. 184). Next to focusing on regions of interest (ROIs), one might want to analyze networks of interest (NOIs; Fedorenko & Thompson-Schill, 2014). Dyslexia and related reading disabilities might arise as a consequence of a problem in the temporal orchestration of activations in the different nodes in the language network. Very likely, in many instances of reading disorders we have to do with impairments in the connectome dynamics of reading and language related areas. Therefore, hereafter I will discuss in more detail the importance of the connection architecture within the language network.

3. Connectivity in the language network

In the classical WLG model Broca's area is connected to Wernicke's area in temporal cortex. On the current view it is generally agreed that the connectivity profile between language-relevant regions in frontal, temporal and parietal cortex is much more extended. Figure 2 gives a schematic overview of the relevant fiber bundles that connect language-relevant brain regions based on diffusion tractography (Amunts & Catani, 2015).

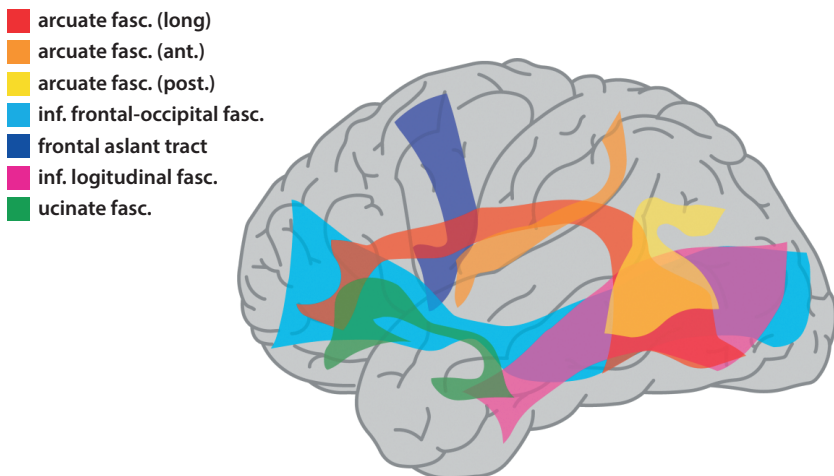


Figure 2. The language network visualized with diffusion tractography. In color, the major anatomical pathways connecting language relevant regions. Hagoort, 2014; after Amunts & Catani (2015)

Another way to characterize connectivity is by means of resting state fMRI. Using this method, Xiang et al. (2010) found a clear topographical functional connectivity pattern in the left inferior frontal, inferior parietal, and temporal regions (see Figure 3). In perisylvian cortex, patterns of functional connectivity obeyed the tripartite nature of language processing (phonology, syntax and semantics). These results are consistent with the view that different parts of Broca's region are involved in, respectively, phonology, syntax, and semantics in connection with areas in inferior parietal and temporal cortex. They revealed a topographical functional organization in the left perisylvian language network, in which areas are most strongly connected according to information type (i.e., phonological, syntactic, and semantic).

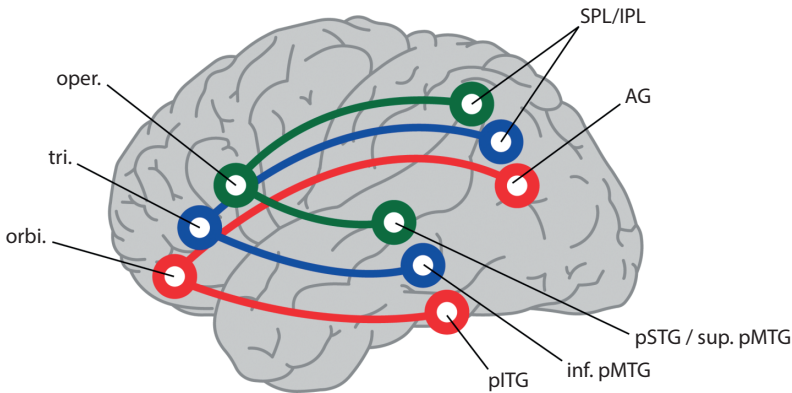


Figure 3. A schematic drawing of the topographical connectivity pattern between frontal and temporal/parietal cortex in the perisylvian language network, as revealed by resting state fMRI (after Xiang et al., 2010). The strongest connections to the pars opercularis (oper.), part triangularis (tri.) and pars orbitalis (orbi.) of Broca's region are shown. SPL/IPL: Superior Parietal Lobule/Inferior Parietal Lobule; AG: Angular Gyrus; pSTG: posterior Superior Temporal Gyrus; sup. pMTG: superior posterior Middle Temporal Gyrus; inf. pMTG: inferior posterior Middle Temporal Gyrus; pITG: posterior Inferior Temporal Gyrus. After Hagoort (2014)

Importantly, Broca's region does not only contribute to unification at the sentence-level, but it is also involved in unification operations at the word level, as in morphological (de)composition (Bozic et al., 2010; Sahin et al., 2009; Hagoort & Levelt, 2009). Compositional and decompositional operations are spatio-temporally extended and occur at multiple levels and at multiple time-slices in the language processing system, but also outside the core language system. Any time lexical and other building blocks enter into the process of utterance interpretation or construction, and any time the linguistic input requires decomposition (presumably

through analysis-by-synthesis) in order to contact the right lexical representations, Broca's region is recruited. The content-specifics of the recruitment are determined by the specific regions and their connectivity profiles, at specific time-slices during processing. As is known for neurons in visual cortex (Lamme & Roelfsema, 2000), the real-time contribution of this region may well vary with time, as a consequence of the different dynamic cortical networks in which it is embedded at different points in time. This fits well with the finding that Broca's region as a whole is not language-specific, but also recruited in the service of other cognitive domains, such as music (Patel, 2003; Kunert et al., 2015) and action (Hamzei et al., 2003), and with the finding that its contribution crosses the boundaries of semantics, syntax, and phonology (Hagoort & Levelt, 2009). Ideally, and in order to make progress, we need to determine both the function and the real-time contribution of Broca's region and the other neural nodes in the language network *at time-slice t in the context of network $N(t)$* .

4. Beyond the classical model

I have outlined the contours of a neurobiological model of language that deviates substantially from the classical WLG model, which was mainly based on lesion and single-word processing data. Three developments are worth highlighting: (1) the connectivity of the language cortex in left perisylvian regions is much more extended than proposed in the classical model and is not restricted to the arcuate fasciculus; (2) the distribution of labor between the core regions in left perisylvian cortex is fundamentally different than proposed in the classical model. It assumes shared circuitry for core aspects of spoken language production and comprehension, which both recruit temporal/parietal regions for retrieval of linguistic information that is laid down in memory during acquisition, and unification of building blocks into utterances or interpretations that are constructed *on-line*. Unification "enables words to cooperate to form new meanings" (Nowak, 2011, p. 179). (3) The operation of language at its full extent requires a much more extended network than what is specified in the classical model, which was mainly based on evidence from single word processing. The basic principle of brain organization for higher cognitive functions is that these are based on the interaction between a number of neuronal circuits and brain regions that support the different contributing functional components. These circuits are not necessarily specialized for language, but nevertheless need to be recruited for the sake of successful language processing. One example is the attention network that might be triggered into operation by specific linguistic devices to safeguard against missing out on the most relevant (new, focused) information in the language input. The other example is the ToM

network that seems crucial for designing our utterances with knowledge of the listener in mind and, as a listener, to make the step from coded meaning to speaker meaning (communicative intent). In addition, the role of the basal ganglia and the fronto-striatal loops in the overarching neurobiological infrastructure for language should not be neglected. Finally, the specific contribution to information processing of any brain region is dependent on its current state as well as the input it receives at any given point in time, which itself depends on the current computational environment in which it is embedded (Hagoort, 2013; Petersson & Hagoort, 2012).

5. Reading as an extension of the language network

As we have seen, the original language network is extended over multiple brain areas. It is this basic configuration that has to be recruited and modified by reading experience. This requires the recruitment of non-language related brain tissue in visual cortex, and the establishment of functional connectivity with the core areas for language. At the same time, modern neuroscience has taught us that brain function is not a one-way street. Reading will hence also impose its structural aspects on the parsing of informational units in the speech input. Moreover, the dynamics of brain processes implies that the temporal orchestration of the visual and phonological activations will turn out to be crucial for accurate, fast reading operations. Reading problems are in part due to problems in the exact orchestration of the nodes in the extended network. Finally, since unification operations are largely shared between reading and listening, my prediction is that once the fast and automatic mappings of orthography onto phonology is well established, most of the higher order unification operations built up for speech will come for free in reading. That is, even if there are symptoms at syntactic processing and sentence-level semantics, very likely they are a consequence of a problem at the decoding stage of orthographic and phonological word forms. Syntactic structure and semantic context might in fact help in compensating for the decoding impairments at lower levels, and could be used to strengthen the connections between word reading and higher order processes. In other words, predictive coding strategies could help in generating stronger templates for the orthographic input, and thereby improve the form representations themselves.

Thanks to the contributions of Ludo Verhoeven, today a more solid connection exists between behavioral and neuroscientific research on reading. This lasting contribution will inspire next generations of researchers to strengthen this connection, and thereby further our understanding of the acquisition of such an intricate cultural invention as reading.

Acknowledgements

This contribution was sponsored by the Spinoza Prize awarded to the author by NWO and the Academy Prize awarded to him by the Royal Netherlands Academy of Arts and Sciences. This contribution is an extension and modification of Hagoort (2014).

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