

MUC (Memory, Unification, Control): A Model on the Neurobiology of Language Beyond Single Word Processing

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28.1 INTRODUCTION

Until not too long ago, the neurobiological model that has dominated our view on the neural architecture of language was the Wernicke-Lichtheim-Geschwind model. In this classical model, the human language faculty was situated in the left perisylvian cortex, with a 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 (LIFC) was claimed to subserve language production. The arcuate fasciculus connected these two areas. This model was based on single word processing. Since then, researchers interested in brain and language have realized that language is more than the concatenation of single words. Research focusing on sentence processing has found that lesions in Broca's region and adjacent cortex impair not only language production but also language comprehension (Caramazza & Zurif, 1976), whereas lesions in Wernicke's region not only affect language comprehension but also language production. More recent neuroimaging studies provided further evidence that central aspects of language production and comprehension are subserved by shared neural circuitry (Menenti, Gierhan, Segaert, & Hagoort, 2011; Segaert, Menenti, Weber, Petersson, & Hagoort, 2012). Since the advent of a whole toolkit of neuroimaging techniques, new models of the neural architecture of human language skills have been proposed. Here, I focus mainly on the Memory-Unification-Control (MUC) model as a model that tries to integrate

knowledge about language processing beyond single words (Hagoort, 2005, 2013). After describing its three components, I discuss the evidence that has accumulated in support of the model.

28.2 MEMORY, UNIFICATION, AND CONTROL

The MUC model distinguishes three functional components of language processing: Memory, Unification, and Control. The Memory component refers to the linguistic knowledge that in the course of language acquisition gets consolidated in neocortical memory structures (see Davis & Gaskell, 2009, for the shift from medial temporal lobe to neocortical structures during consolidation). It is the only language-specific component of the model. The knowledge about the building blocks of language that is stored in memory (e.g., phonological, morphological, syntactic building blocks; jointly referred to as lexical items) is domain-specific and, hence, coded in a format that is different from, for example, color and visual object information.

However, language processing is more than memory retrieval and more than the simple concatenation of retrieved lexical items. The expressive power of human language derives from being able to combine elements from memory in novel ways. This process of deriving higher-level (i.e., sentence and beyond) meaning is referred to as Unification. Although as a result of the Chomskyan revolution in linguistics psycholinguistic studies of unification have mainly focused on

syntactic analysis, unification operations not only take place at the syntactic processing level but also are a hallmark of language across representational domains (Jackendoff, 2002). Thus, at the semantic and phonological levels, lexical elements are combined and integrated into larger structures. Hence, I distinguish between syntactic, semantic, and phonological unification (Hagoort, 2005).

Finally, the Control component relates language to joint action and social interaction, and it is invoked, for instance, when the contextually appropriate target language has to be selected, or for handling the joint action aspects of using language in conversational settings. Later, it is shown how languages have built-in linguistic devices that trigger the attentional control system into operation.

In the MUC model, the distribution of labor is as follows (Figure 28.1). Regions in the temporal cortex (in yellow) and the angular gyrus in parietal cortex subserve the knowledge representations that have been laid down in memory during acquisition. These regions store information, including phonological word forms, morphological information, word meanings, and the syntactic templates associated with noun, verbs, and adjectives (for details, see Hagoort, 2003, 2005, 2009). Dependent on knowledge type, different parts of temporal cortex are involved. Frontal regions (Broca's area and adjacent cortex; in blue) are crucial for unification operations. These operations generate larger structures from the building blocks that are

retrieved from memory. Within LIFC (Unification Space), there seems to be a certain spatial distribution of recruitment dependent on the type of information that gets unified. Semantic unification recruits BA 47 and BA 45; syntactic unification has its focus in BA 45 and BA 44; phonological processes recruit BA 44 and ventral parts of BA 6 (Hagoort & Indefrey, 2014). In addition, executive control needs to be exerted such that the correct target language is selected, turn-taking in conversation is orchestrated, attention is given to the most relevant information in the input, and so forth. Control regions involve dorsolateral prefrontal cortex (in pink) and midline structure, including the anterior cingulate cortex and the parts of parietal cortex that are involved in attention (not shown in Figure 28.1).

The distribution of labor in the MUC model is not absolute. Language functions do not reside in single brain regions. Instead, language is subserved by dynamic networks of brain regions, including the ones outlined here. Ultimately, the mapping of a given language function onto the neural architecture of the brain is in terms of a network of brain areas instantiating that particular language function (McIntosh, 2008; Mesulam, 1998; Sporns, 2011). This is what Fedorenko and Thompson-Schill (2014) refer to as Networks of Interest. Typically, each node in such a network will participate dynamically in other functional networks as well. Although one can claim a certain contribution of a specific region (e.g., part of Broca's area), it is crucial to realize that such a contribution depends on the interaction with other regions that are part of the network. 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). Therefore, before discussing the empirical evidence for the distribution of labor within the MUC framework, I discuss the connectivity profile of the language networks in the brain.

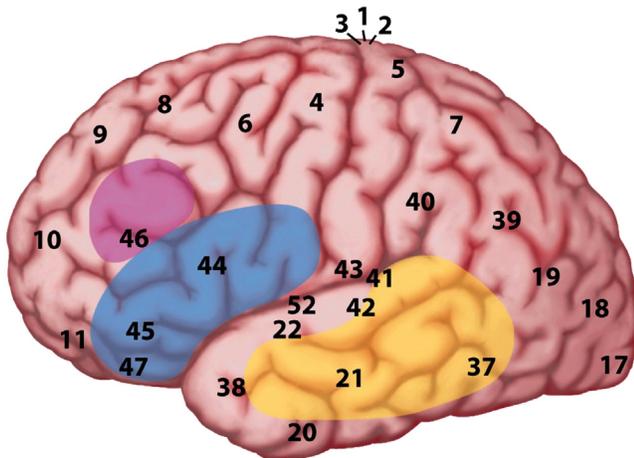


FIGURE 28.1 The MUC model of language. The figure displays a lateral view of the left hemisphere. The numbers indicate Brodmann areas. These are areas with differences in the cytoarchitectonics (i.e., composition of cell types). The memory areas are in the temporal cortex (in yellow) including the angular gyrus in parietal cortex. Unification requires the contribution of Broca's area (Brodmann areas 44 and 45) and adjacent cortex (Brodmann areas 47 and 6) in the frontal lobe. Control operations recruit another part of the frontal lobe (in pink) and the anterior cingulate cortex, as well as areas involved in attention (not shown in the figure).

28.3 THE NETWORK TOPOLOGY OF THE LANGUAGE CORTEX

The classical model has given the arcuate fasciculus a central role in connecting the language-relevant parts of the brain. This was based on the idea that Broca's area and Wernicke's area were the two central nodes in the language network. The language network is much more extended than was assumed in the classical model and includes not only regions in the left hemisphere but also the right hemisphere areas. However, the evidence of additional activations in the right hemisphere and areas other than Broca's and Wernicke's does not take away the crucial role of left

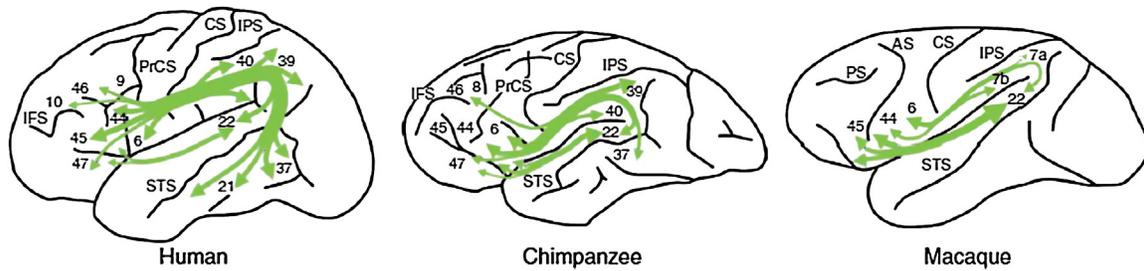


FIGURE 28.2 The arcuate fasciculus in a human, chimpanzee, and macaque in a schematic lateral view of the left hemisphere. From *Rilling et al. (2008)*, courtesy of Nature Publishing Group.

perisylvian cortex. In a recent meta-analysis based on 128 neuroimaging studies, *Vigneau et al. (2010)* compared left and right hemisphere activations observed in relation to language processing. For phonological processing, lexico-semantic processing, and sentence or text processing, the number of activation peaks in the right hemisphere comprised less than one-third of the activation peaks in the left hemisphere. Moreover, in the majority of cases the right hemisphere activations were found in homotopic regions, suggesting a strong interhemispheric dependency. It is therefore justified to think that for the majority of the human population (e.g., with the exception of some portion of left-handers, cases of left hemispherectomy), the language-readiness of the human brain is strongly but not exclusively based on the organization of the left perisylvian cortex. This, however, does not deny the relevant contributions of the right hemisphere in, for instance, speech recognition (*Hickok & Poeppel, 2007*).

A recent technique for tracing fiber bundles in the living brain is diffusion tensor imaging (DTI). Using DTI, *Rilling et al. (2008)* tracked the arcuate fasciculus in humans, chimpanzees, and macaques. These authors found in humans a prominent temporal lobe projection of the arcuate fasciculus that is much smaller or absent in nonhuman primates (*Figure 28.2*). Moreover, connectivity with the middle temporal gyrus (MTG) was more widespread in the left than in the right hemisphere. This human specialization may be relevant for the evolution of language. *Catani et al. (2007)* found that the human arcuate fasciculus is strongly lateralized to the left, with quite some variation on the right. On the right, some people lack an arcuate fasciculus, in others it is smaller in size, and only in a minority of the population is this fiber bundle of equal size in both hemispheres. This pattern of lateralization was confirmed in a study involving 183 healthy right-handed volunteers in the age range between 5 and 30 years (*Lebel & Beaulieu, 2009*). The functionality of the arcuate fasciculus is not limited to single word processing. In a recent work, *Wilson, Galantucci, Tartaglia, and Gorno-Tempini (2012)* reported syntactic deficits in patients with primary

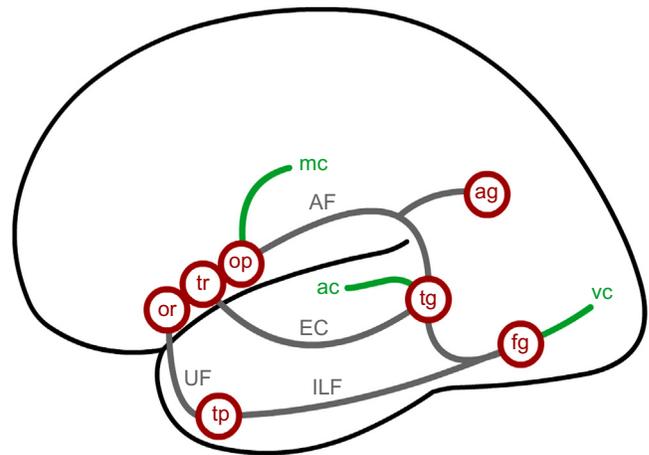


FIGURE 28.3 Simplified illustration of the anatomy and connectivity of the left hemisphere language network. Cortical areas are represented as red circles: pars orbitalis (or), pars triangularis (tr), and pars opercularis (op) of the LIFC, angular gyrus (ag), superior and middle temporal gyri (tg), fusiform gyrus (fg), and temporal pole (tp).

progressive aphasia after damage to the dorsal tracts but not after damage to the ventral tracts. This suggests that the dorsal tracts, including the arcuate fasciculus, are a key component in connecting frontal and temporal regions involved in syntactic processing. Again, exclusivity is difficult to establish. Part of these tracts might also subserve other aspects of language processing.

In addition to the arcuate fasciculus, other fiber bundles are important in connecting frontal with temporoparietal language regions (*Figure 28.3*). These include the superior longitudinal fasciculus (adjacent to the arcuate fasciculus) and the extreme capsule fasciculus, as well as the uncinate fasciculus, connecting Broca's area with superior and middle temporal cortex along a ventral path (*Anwander, Tittgemeyer, von Cramon, Friederici, & Knosche, 2007; Friederici, 2009; Kelly et al., 2010*). *Figure 28.3* provides a schematic overview of the more extended connectivity profile of the left perisylvian cortex.

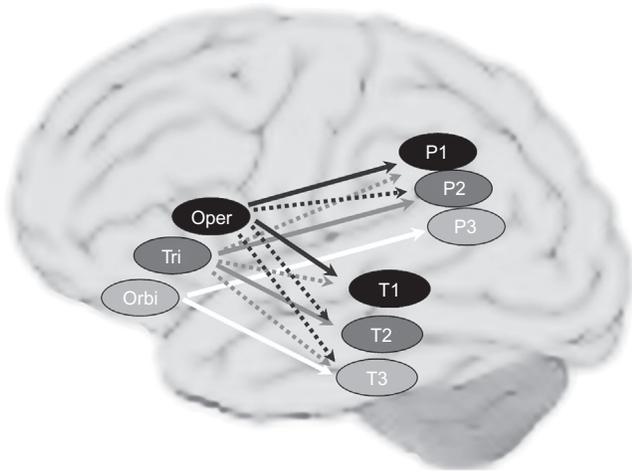


FIGURE 28.4 The topographical connectivity pattern between frontal and temporal/parietal cortex in the perisylvian language networks. Connections to the left pars opercularis (oper), pars triangularis (tri), and pars orbitalis (orbi) are shown in black, dark grey, and white arrows, respectively. The solid arrows represent the main (most significant) correlations and the dashed arrows represent the extending (overlapping) connections. Brain areas assumed to be mainly involved in phonological, syntactic, and semantic processing are shown in black, dark grey, and light grey circles, respectively. P1, supramarginal gyrus; P3, angular gyrus (AG); P2, the area between SMG and AG in the superior/inferior parietal lobule; T1, posterior superior temporal gyrus; T2, posterior MTG; P3, posterior inferior temporal gyrus.

Using resting state fMRI, Xiang, Fonteijn, Norris, and Hagoort (2010) found a clear topographically organized connectivity pattern in the left inferior frontal, parietal, and temporal regions (Figure 28.4). In the left—but not in the right—perisylvian cortex, functional connectivity patterns obeyed the tripartite nature of language processing (phonology, syntax, and semantics). These results support the assumption of the functional division for phonology, syntax, and semantics of the LIFC, including Broca’s area, and 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). The dorsal pathways might be more relevant for phonological and syntactic processing, whereas the ventral pathways seem to be involved in connecting regions for semantic processing.

28.4 THE EMPIRICAL EVIDENCE FOR THE MUC MODEL

We have seen that there is a much more widespread connectivity profile in left perisylvian language cortex than was assumed in the classical model. The MUC model deviates from the classical model in the division

of labor between Broca’s area, Wernicke’s area, and adjacent regions. However, the proposed distribution of labor is not absolute, but rather embedded and situated in the network skeleton of the language system’s neural architecture.

What is the evidence for the relative division of labor proposed in the MUC model? Let us consider the syntactic network first. In comparison with phonological and semantic processing, which have compelling bilateral contributions, syntactic processing seems strongly lateralized to the left hemisphere perisylvian regions. Indirect support for a distinction between a memory component (i.e., the mental lexicon) and a unification component in syntactic processing comes from neuroimaging studies on syntactic processing. Two regions have been systematically reported in relation to syntactic processing (Hagoort & Indefrey, 2014): the left posterior superior/middle temporal gyrus (STG/MTG) and the LIFC. The left posterior temporal cortex is known to be involved in lexical processing (Hickok & Poeppel, 2004, 2007; Indefrey & Cutler, 2004; Lau, Stroud, Plesch, & Phillips, 2006). In connection to the MUC model, this part of the brain might be important for the retrieval of the syntactic frames that are stored in the lexicon. The idea of syntactic frames that specify the possible local syntactic environment of a given lexical item is in line with linguistic and computational approaches that assume syntactic knowledge to be lexically specified (Culicover & Jackendoff, 2006; Joshi & Schabes, 1997; Vosse & Kempen, 2000). The Unification Space, where individual frames are connected into a phrasal configuration for the whole utterance, might recruit the contribution of LIFC.

Direct empirical support for this distribution of labor between LIFC (Broca’s area) and temporal cortex was found in a study of Snijders et al. (2009). These authors performed an fMRI study in which participants read sentences and word sequences containing word-category (noun-verb) ambiguous words (e.g., “watch”) and the same materials with the unambiguous counterparts of the lexical-syntactic ambiguities. The ambiguous items were assumed to activate two independent syntactic frames, whereas the unambiguous counterparts result in the retrieval of only one syntactic frame. Solely based on a computational model of syntactic processing (Vosse & Kempen, 2000) and the hypothesized contribution of temporal and frontal cortex regions, it was predicted that the regions contributing to the syntactic unification process should show enhanced activation for sentences compared with words, and only within sentences should they display a larger signal for ambiguous than for unambiguous conditions. The posterior LIFC showed exactly this predicted pattern, confirming the hypothesis that

LIFC, particularly BA 44 and BA 45, contributes to syntactic unification. The left posterior MTG was activated more for ambiguous than unambiguous conditions, as predicted for regions subserving the retrieval of lexical-syntactic information from memory. It thus seems that the LIFC is crucial for syntactic processing in conjunction with the left posterior MTG, a finding supported by patient studies with lesions in these very same regions (Caplan & Waters, 1996; Rodd, Longe, Randall, & Tyler, 2010; Tyler et al., 2011). Presumably these regions are connected via the dorsal pathways.

In addition to syntactic unification, there is the need for semantic unification. One aspect of semantic unification is filling the slots in an abstract event schema. Semantic processing also recruits a left perisylvian network, albeit with a substantially weaker lateralization profile than syntactic processing. A series of fMRI studies aimed to identify the semantic processing network. These studies either compared sentences containing semantic/pragmatic anomalies with their correct counterparts (e.g., Friederici, Ruschemeyer, Hahne, & Fiebach, 2003; Hagoort, Hald, Bastiaansen, & Petersson, 2004; Kiehl, Laurens, & Liddle, 2002; Ruschemeyer, Zysset, & Friederici, 2006) or compared sentences with and without semantic ambiguities (Davis et al., 2007; Hoening & Scheef, 2005; Rodd, Davis, & Johnsrude, 2005). In the latter case, there are multiple word meanings for a given lexical item that will induce competition and selection in relation to filling a particular slot in the event schema. As with syntactic unification, the availability of multiple candidates for a slot will therefore increase the unification load. In the case of the lexical-semantic ambiguities, there is no syntactic competition. Increased processing is therefore attributable to unification of meaning instead of syntax. The most consistent finding across studies on semantic unification is the activation of the LIFC, particularly BA 47 and BA 45 (Hagoort & Indefrey, 2014).

A further indication for the contribution of LIFC in semantic unification comes from a few studies investigating semantic unification of multimodal information with language. Using fMRI, Willems, Özyürek, and Hagoort (2007) assessed the neural integration of semantic information from spoken words and from co-speech gestures into a preceding sentence context. Spoken sentences were presented in which a critical word was accompanied by a co-speech gesture. Either the word or the gesture could be semantically incongruous with respect to the previous sentence context. Both an incongruous word as well as an incongruous gesture led to increased activation in LIFC (BA 45/47) as compared with congruous words and gestures (for a similar finding with pictures of objects, see Willems, Özyürek, & Hagoort, 2008). This supports the claim

that LIFC is a key node in the semantic unification network, unifying semantic information from different modalities.

From these findings it seems that syntactic and semantic unification is realized in a dynamic interplay between LIFC as a multimodal unification site and also knowledge-specific regions. Again, it is important to stress that the interplay of these regions is crucial to realize the functional component of unification.

In other models, the anterior temporal lobe has been argued to be relevant for combinatorial operations (Hickok & Poeppel, 2007; Rogalsky et al., Chapter 47 of this volume). One possibility is that this is limited to conceptual combinations for which the mapping of grammatical roles (e.g., subject, object) onto thematic roles (e.g., agent, patient) is not required (Baron & Osherson, 2011). In the latter case, the contribution of Broca's region is presumably highly relevant.

28.5 A GENERAL ACCOUNT OF THE ROLE OF LIFC IN LANGUAGE PROCESSING

So far, we have seen that LIFC plays a central role in syntactic and semantic unification processes, albeit with different activation foci for these two types of unification. However, there is convincing evidence that LIFC also plays a role beneath the phrasal and sentence level. It is found to contribute to decomposition and unification at the word level. Words are not processed as unstructured, monolithic entities. Based on the morpho-phonological characteristics of a given word, a process of lexical decomposition takes place in which stems and affixes are separated. For spoken words, the trigger for decomposition can be something as simple as the inflectional rhyme pattern, which is a phonological pattern signaling the potential presence of an affix (Bozic, Tyler, Ives, Randall, & Marslen-Wilson, 2010). Decomposing lexical input appears to be a ubiquitous and mandatory perceptual strategy; that is, decompositional processes are triggered not only for words with obvious parts (e.g., work-ed) but also for semantically opaque words (e.g., bell-hop) and even nonwords with putative parts (e.g., blicket-s, blicket-ed). In a series of fMRI studies on the processing of inflectional morphology, Bozic et al. (2010) have found that LIFC, especially BA 45, subserves the process of morphological decomposition. Intracranial recordings in BA 45 from epileptic patients during pre-surgical preparation indicate that the same brain area is also involved in the generation of inflected forms during language production (Sahin, Pinker, Cash, Schomer, & Halgren, 2009; see also comments by Hagoort & Levelt, 2009).

The evidence for LIFC involvement at word- and sentence-level processing in both production and comprehension results in the question of how to account for its role more generally. This is still an open issue, but there is a possible answer. Notwithstanding the division of labor within LIFC, its overall contribution can be characterized in more general terms than hierarchical or even sentence-level processing. Instead, the LIFC is most likely involved in unification operations at the word and sentence level, in connection with temporal and parietal regions that are crucial for memory retrieval (Hagoort, 2005). Compositional and decompositional operations occur at multiple levels and at multiple time slices in the language processing system, but also outside the language system. Any time lexical and other building blocks enter into the process of utterance interpretation or construction, and any time the input string requires decomposition (presumably through analysis-by-synthesis) to contact the right lexical representations, LIFC is recruited.

This view is fully compatible with recent accounts in linguistics that view both morphology and syntax to involve the retrieval of pieces of stored structure with variables (Jackendoff, personal communication, 2014). Hence, no principled distinction is claimed between unification operations in syntax and morphology.

This account of LIFC's contribution is more general than is claimed in other models. For example, proposals have been made that LIFC (Broca's area) has a more specialized role in language processing, has more to do with linguistically motivated operations of syntactic movement (Grodzinsky & Santi, 2008), and is more involved in the processing of hierarchical structures (Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006). However, such proposals are difficult to reconcile with the LIFC contributions to morphological processes. Hence, the account specified here seems to have more empirical support.

28.6 THE DYNAMIC INTERPLAY BETWEEN MEMORY AND UNIFICATION

Although a connection is made between functional components of the cognitive architecture for language and specific brain regions, this is an idealization of the real neurophysiological dynamics of the perisylvian language network. Crucially, for language as for most other cognitive functions, the functional contribution of any area or region has to be characterized in the context of the network as a whole, where specialization of any given node is only relative and realized in a dynamic interaction with the other nodes in the network (Mesulam, 1990, 1998). How this can be viewed is specified in more detail for semantic

unification by way of illustrating the principle of dynamic interaction.

In posterior and inferior temporal and parietal (angular gyrus) regions, neuronal populations are activated that represent lexical information associated with the incoming word, including its semantic features. From here, neural signals can follow two routes. The first exploits local connectivity within these posterior regions, resulting in a graded activation of neighboring neuronal populations, coding for related lexical-semantic information. Such local spread of activation contributes to setting up a lexical-semantic context in temporo-parietal cortex (Figure 28.5, green circle). The second route is based on long-distance connections to LIFC, through direct white matter fibers, resulting in the selective activation of populations of frontal cortex neurons. These will respond with a self-sustaining firing pattern (see Durstewitz, Seamans, & Sejnowski, 2000 for a review). Efferent signals in this case can only take the long-range route back. The most parsimonious account here is that frontal neurons will send efferent signals back to the same regions in temporo-parietal cortex from where afferent signals were received. This produces another spread of activation to neighboring temporo-parietal regions, which implies that connections representing a given semantic

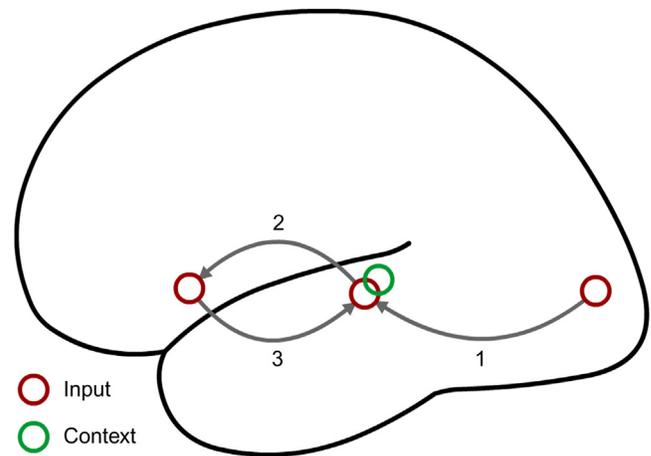


FIGURE 28.5 Processing cycle subserving semantic unification in the left hemisphere language network. Inputs are conveyed from sensory regions (here visual cortex) to the inferior, middle, and superior temporal gyri (1), where lexical information is activated. Signals are hence relayed to the inferior frontal gyrus (2), where neurons respond with a sustained firing pattern. Signals are then fed back into the same regions in temporal cortex from where they were received (3). A recurrent network is thus set-up, which allows information to be maintained online, a context (green circle) to be formed during subsequent processing cycles, and incoming words to be unified within the context. At each processing cycle a balance is achieved by letting input-driven activity find attractor states, that is, the maximum possible overlap with active populations in temporal cortex.

context will be strengthened. During each word processing cycle, the memory (temporo-parietal) and unification (inferior frontal) components interact by letting activation reverberate through the circuit in [Figure 28.5](#). Achieving the necessary outcomes for language comprehension may be more or less demanding, depending on how close the relation is between input and context.

28.7 ATTENTIONAL CONTROL

The third component in the MUC model is referred to as Control. One form of control is attentional control. In classical models of sentence comprehension—of either the syntactic-structure-driven variety ([Frazier, 1987](#)) or in a constraint-based framework ([Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995](#))—the implicit assumption is usually that a full phrasal configuration results and a complete interpretation of the input string is achieved. However, often the listener interprets the input on the basis of bits and pieces that are only partially analyzed. As a consequence, the listener might overhear semantic information (the Moses illusion; [Erickson & Mattson, 1981](#)) or syntactic information (the Chomsky illusion; [Wang, Bastiaansen, Yang, & Hagoort, 2012](#)). In the question “How many animals of each kind did Moses take on the ark?”, people often answer “two,” without noticing that it was Noah who was in command of the ark, not Moses. It was found that syntactic violations might not trigger a brain response if they are in a sentence constituent that provides no new information ([Wang et al., 2012](#)). [Ferreira, Bailey, and Ferraro \(2002\)](#) introduced the phrase “good-enough processing” to refer to the listeners’ and readers’ interpretation strategies. In a good-enough processing context, linguistic devices that highlight the most relevant parts of the input might help the listener/reader in allocating processing resources optimally. This aspect of linguistic meaning is known as “information structure” ([Buring, 2007](#); [Chafe, 1976](#); [Halliday, 1967](#); [Krifka, 2007](#)). The information structure of an utterance essentially focuses the listener’s attention on the crucial (new) information in it. In languages such as English and Dutch, prosody plays a crucial role in marking information structure. For instance, in question–answer pairs, the new or relevant information in the answer will typically be pitch accented. After a question like “What did Mary buy at the market?”, the answer might be “Mary bought VEGETABLES” (accented word in capitals). In this case, the word “vegetables” is the focus constituent, which corresponds to the information provided for the Wh-element in the question. In a recent fMRI study ([Kristensen, Wang, Petersson, & Hagoort, 2013](#)), we

tested the idea that pitch accent, which in Dutch is used to mark certain information as focus, recruits attentional networks in the service of more extended processing of the most relevant information. In our study, the attentional network was first localized in an auditory nonverbal attention task. This task activated, as expected, bilateral superior and inferior parietal cortex. In the language task, participants were listening to sentences with and sentences without semantic-pragmatic anomalies. In half of the cases these anomalies and their correct counterparts were marked as in focus by a pitch accent; in the other half of the cases they were not. The results showed an interaction in bilateral inferior parietal regions between prosody (pitch accent) and congruence; for incongruent sentences, but not for congruent ones, there was larger activation if the incongruent words carried a focus marker (i.e., the pitch accent).

Overall, the activation overlap in the attention networks between the localizer task and the sentence processing task indicated that marking of information structure modulated a domain-general attention network. Pitch accent signaled the saliency of the focused words and thereby recruited attentional resources for extended processing. This suggests that languages might have developed built-in linguistic devices (i.e., focus markers) that trigger the recruitment of attentional systems to safeguard against the possibility that in a good-enough processing system the most relevant information might go unnoticed. This provides one example of the interaction between a general demand/control system ([Fedorenko, Duncan, & Kanwisher, 2012](#)) and the core components of the language network.

28.8 BEYOND THE CLASSICAL MODEL

I have outlined the contours of a neurobiological model of language that is a substantial augmentation of the classical Wernicke-Lichtheim-Geschwind model, which was a model for single word processing mainly based on lesion and patient data.

Three major additions are worth highlighting. First, the connectivity of the language cortex in left perisylvian regions is much more extended than proposed in the classical model and is certainly not restricted to the arcuate fasciculus. Second, the distribution of labor between the core regions in left perisylvian cortex is not one in terms of production and comprehension. Shared circuitry has been established for core aspects of language production and comprehension. Both recruit temporal/parietal regions for retrieval of linguistic information that is laid down in memory during acquisition and LIFC for unification of building blocks into

utterances or interpretations that are constructed online. Unification “enables words to cooperate to form new meanings” (Nowak, 2011, p. 179). Third, the operation of language in its full glory requires a much more extended network than what the classical model contained, 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; nevertheless, they need to be recruited for the sake of successful language processing. One example is the general attentional networks 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. Another example, not further discussed here, is the Theory of Mind network that seems crucial for designing our utterances with knowledge of the listener in mind or, as a listener, to make the step from coded meaning to speaker meaning (Bašnáková, Weber, Petersson, van Berkum, & Hagoort, 2013; Hagoort & Levinson, 2015).

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