

Brain and Language: Insights from Aphasia and Brain Imaging Data

Abdul-Malik Othman Esmail Ghaleb *

Abstract

Attempts to understand the relationship between language and the brain have a long history. Prior to the advent of functional imaging, the history of aphasiology has been the most important piece of evidence to show how language functions are represented in the human brain. Recently, a great deal of progress on brain-language research has been driven by advances in both linguistics and cognitive neuroscience. These distinct approaches, coupled with the use of in-vivo imaging procedures have prompted significant insights into the neural mechanisms that underlie language. Despite the fact that scientific inquiry into brain-language relationship has grown substantially to support the neurological basis of language, there is still much controversy with respect to its organization in the human brain. This paper, therefore, offers an overview of the current state of knowledge on topics related to the neural and functional representation of language based on findings from neuropsychological and latest neuroimaging studies. The paper concludes by discussing the implications of this research for the nature of language representation and processing in the brain.

Key words: Aphasia, Modularity, Neuroimaging, Broca's area, Language Networks

1. Introduction

One of the most challenging issues related to human language is understanding how it is organized and processed in the brain. In fact, a century and a half after the initial discoveries of lateralization of language, the neural basis for language is still not clearly understood. Moreover, as part of this incomplete knowledge, the relationship between cortical brain areas involved in language and language processing is less well known compared to many other brain functions (e.g., the motor visual systems). Amunts (2008) points out that one particular reason for this difference is the fact that human language is very complex in comparison to other cognitive functions, and the lack of agreement among psycho- and neurolinguistics as to how this function should be analyzed and consequently be related to the underlying anatomy. Nevertheless, in more recent years, advances in both linguistics and cognitive neuroscience together with rapid development of functional imaging techniques have provided intriguing insights into the nature of the representation of language, the processes involved in language, and its underlying neural organization (for review and new perspectives, see Altmann, 2002; Basso, 2003; Hickok & Poeppel 2004; Ghaleb, 2007). Current practice in psycholinguistic and neurolinguistic research uses the available methods, analytic approaches and technologies to reveal the neural architecture and processes underpinning language, with the following broad areas of interest:

- What are the neural underpinnings of language?
- Are these neurocognitive correlates dedicated to language?
- How is language represented in the brain?
- Do different parts of language and/or processes depend on distinct areas of the brain?

* Department of English Language and Literature
Faculty of Arts, Taiz University, Yemen

- Can neurolinguistic evidence be used to support existing theoretical models of language processing and/or production?

This field of study is relatively new, and there are considerable gaps in our knowledge. Even so, evidence from the available studies provides a starting point for examining these questions. This paper, therefore, attempts to review the current state of knowledge of the neural and functional organization of language. It reviews and interprets data derived from aphasiology studies as well as neuroimaging studies, that bear on this topic. The paper is organized as follows. First, I present a brief overview of the human cerebral cortex. Following a brief description of basic methods of studying language-brain relationships, and a brief review of current models of the functional organization of language in the brain. I then review and discuss the neural and functional organization of language, with reference to neuropsychological and contemporary neuroimaging studies on aspects of language processing. In this section, I focus on the impact of the findings of these studies on the evidence for the localized versus the distributed nature of the neural substrate for language functions. I then briefly discuss the role of Broca's area in language processing, based on data from recent neuropsychological and brain imaging studies, and outline an alternative way of looking at the function of Broca's area, with concluding remarks on the implications of this research for the nature of language representation and processing in the human brain.

1.1. A Brief Overview on the Human Cerebral Cortex

The cortex consists of two halves called the cortical hemispheres; and each hemisphere can be subdivided into four lobes (frontal, parietal, occipital, and temporal), which maintain their relative positions. Two major landmarks indicate boundaries between lobes. The central sulcus, or fissure is the boundary between the frontal and the parietal lobes, and the Sylvian fissure separates the temporal lobe from both frontal and parietal lobes. The Sylvian fissure is important as a landmark, because all of the most relevant areas for language are located in its close vicinity. The areas next to the Sylvian fissure are called the perisylvian areas. Figure (1) shows a lateral view of the left hemisphere with its most common area subdivision. These areas have been proposed by Brodmann (1909) and reflect neuroanatomical properties of the cortical gray matter (Pulvermüller, 2002).

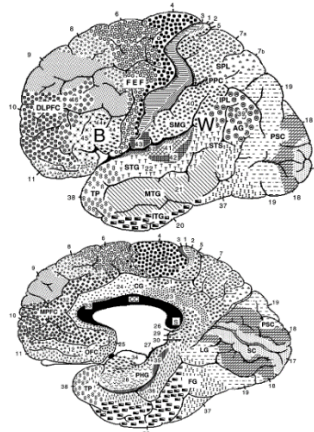


Figure 1: A representation of the cortical map of Brodmann, which distinguishes regions of the cortex on the basis of their microscopic features. AG, angular gyrus; B, Broca's area; CC, corpus callosum; CG, cingulate cortex; DLPFC, dorsolateral prefrontal cortex; FEF, frontal eye fields (premotor cortex); FG, fusiform gyrus; IPL, inferior parietal lobule; ITG, inferior

temporal gyrus; LG, lingual gyrus; MPFC, medial prefrontal cortex; MTG, middle temporal gyrus; OFC, orbitofrontal cortex; PHG, parahippocampal gyrus; PPC, posterior parietal cortex; PSC, peristriate cortex; SC, striate cortex; SMG, supramarginal gyrus; SPL, superior parietal lobule; STG, superior temporal gyrus; STS, superior temporal sulcus; TP, temporopolar cortex; W, Wernicke's area. Adapted from Mesulam (2002).

As reviewed by Moro (2008) the cerebral cortex includes an intricate net of neurons that transmit electric impulses to each other through the white matter. These neurons are much smaller than pyramidal cells, and make only local connections and receive input from many adjacent pyramidal cells. The small inhibitory cells can dampen down cortical activity in case too many of their adjacent excitatory pyramidal cells become active at one time. As the cerebral cortex plays a fundamental role in cognitive processes, all such processes depend on the cortical activity of neurons. The number of cortical neurons in the brain is estimated at 100 billion, and the number of synapses in the cortex may be an astonishing 1 million billion. The computational power made possible by this extraordinary number of connections renders the cortex the site of the most advanced functions of the human brain. This astonishing fact alone, together with the complexity of these nets, illustrates well the complexity of uncovering the neural mechanism underlying language function. This is also why some eminent scientists disregard the possibility of our ever understanding the mechanism of cognitive processes.

1.2. Methods of Exploring Brain-Language Relationships

There are two general methods in the study of the neurology of language and in the study of brain-language relations: behavioral studies and functional imaging. Behavioral studies typically use aphasia (that is, lesion studies) as a window into the normal system. Until the onset of functional imaging techniques (Petersen *et al.*, 1989), most knowledge concerning the neural correlates of language processing was derived from neuropsychological investigation of language pathology subsequent to brain damage or by electrical stimulation and recording from individuals undergoing neurosurgery. Neuroimaging studies of cognitive function have looked to lesion studies for confirmation of the functional organization of the brain. The advances in neuroimaging methods has provided researchers with a powerful, noninvasive means to examine brain activity during processing of linguistic stimuli. This activity can be measured while people read or listen to sets of words or sentences with ERPs (Event-Related Potentials), PET (Positron Emission Tomography) scans, and fMRI (functional Magnetic Resonance Imaging) scans. This type of data have offered the promise that the neural underpinnings for cognitive functions, especially those related to language processing, could now be explored in living, healthy subjects. Furthermore, this method seem capable of enabling researchers to explore the functional abnormalities in patients with various kinds of language disorders (Amunts 2008). Since then the potential to assess how brain regions interact to implement specific neurolinguistic and other cognitive functions has necessitated the development of network analysis methods, and has given rise to a new paradigm in which cognitive functions are conceived as being mediated by distributed interacting neural elements (for more information see review by Horwitz, Tagamets & McIntosh, 1999).

An important issue to consider here concerns the interpretation of lesion studies and functional imaging results. This point needs to be understood very well because it will be crucial when we deal with the findings from neuropsychological, and functional imaging research on language processing. In a highly thoughtful review of how the results of fMRI and PET studies are interpreted, Bub (2000:482) pointed out that "functional imaging is confronted with a host of methodological difficulties that must be navigated successfully before the technique can be used to provide a testing ground for neuropsychological and neurophysiological theories of higher cognitive function."

Bub (2000: 468) argues that one should not be seduced by “the hidden tendency to assume that the pattern of activation seen in the final image is a literal description of neurons firing to a particular task demand.” It is important to appreciate that if the same region of the brain is activated to the same extent in both a “control” condition and an “experimental” condition, this will not show up as a regional difference when the two conditions are compared. That is, lack of PET activation does not mean lack of brain activity. Thus the patterns of activation reported in published papers do not necessarily identify in their entirety those neural areas involved in a given task. Moreover, “a pattern of significantly activated brain areas does not provide information about the interregional relationships” (Karbe *et al.*, 1998: 114–115). Distinguishing those regions that are differentially activated in two or more experimental conditions may shed little or no light on the total functional organization or brain circuitry involved in particular cognitive operations.

1.3. Models of Brain Organization for Language

A central question in psycholinguistic research which has always been hotly debated for centuries, and which is still much discussed at present, is whether certain linguistic abilities result from dedicated brain areas each specialized for specific kinds of linguistic representations and processes, as characterized by some of the proponents of this phrenological or modular view (Fodor 1983), or whether these abilities are more accurately described in terms of interactions among different linguistic levels distributed across multiple brain regions (interactive or distributive view) as proposed by other leading scholars (McClelland & Rumelhart, 1986; Seidenberg & McClelland, 1989).

Researchers favoring the modularity perspective have assumed a set of distinct processing components within a modular system (e.g., the lexicon or grammar), each subserving a language-specific function and operating on language-specific information and representations (e.g., Fodor, 1983; Grodzinsky, 1995a, 1995b, 2000; Maunder, Fromkin, & Cornell, 1993; Pinker, 1994; Pinker & Ullman, 2002). Such proposals assume a static base of linguistic knowledge which is associated with distinct neural structures. The origins of these claims lie in Franz Gall (1809) and his collaborator Spurzheim who conceived of the brain as composed of several independent organs, each subserving a specific faculty. As a result, the neural organization of language has long been considered to be largely modular. However, this rigid modular view has been reviewed and renounced in recent times by two important developments in neuroscience. The first is the development of distributive or connectionist models of brain function, emphasizing circuits, parallel processing, and the cortical-subcortical representations of functions discussed in the previous section. The second is the information from studies using modern brain imaging techniques to visualize cerebral activity of various functions, including language.

The distributive models have offered an alternative to an understanding of brain function based on neural network and parallel distributed processing (PDP), with an emphasis on cortical-subcortical and right and left hemisphere cooperation and coordination in normal brain functioning (e.g., Nadeau, 2012). According to the prevailing connectionist model (e.g., Pulvermüller 2003), individual concepts are represented by a pattern of activation existing across a large network of interconnected nodes approximately analogous to the synaptic connections among individual neurons. No individual node corresponds to any concept; every concept is represented by a pattern of widely distributed nodes. Instead of one node activating another one in turn, all nodes are activated in parallel, and each passes activation to each of the others. In this view, complex functions like language emerge from the conjoint activity of many brain regions which may be spatially discontinuous and widely distributed. A given region may be relevant for language, participate in language, and even be essential for language, but its

relationship to language is not transparent, nor is it dedicated exclusively to the processing of language or any of its subcomponents. Instead, the regions involved in language processing are also involved in the mediation of processes that language shares with other domains, including specific forms of memory, attention, perception and motor planning. This perspective makes a number of predictions about the nature of language processing in normal and language-impaired populations. Rather than being restricted to a set of specialized neural substrates, language processes should engage multiple distributed brain areas, which may be involved in a variety of cognitive functions that are not specific to language.

Certainly the underlying assumptions are at odds: the modular distinction account suggests that brain regions are specialized for particular language operations, while the distributive account claims that language requires collaboration from the conjoint activity of spatially discontinuous and widely distributed brain regions. That is, they disagree about “whether there are domain-specific modules associated with different components of the grammar, whether such modules recruit distinct neural structures that are solely dedicated to the processing of that module and whether the neural systems associated with language are different from those recruited across other cognitive domains” (Blumstein & Amso, 2013: 45). Findings from aphasiology and neuroimaging might help us to resolve this disagreement. In the next sections, findings from studies of adult aphasia and brain imaging studies on language processing in adults are selectively discussed. We begin by introducing the brain regions commonly known to be involved in language processing.

2. Brain Regions involved in Language

The part of the brain most relevant for language is the cerebral cortex (Pulvermüller, 2002). This fact has been proved by neurological observations, in particular, the fact that lesions in certain areas of the cortex lead to neurological language impairment, aphasia (Broca, 1861/1977). The main conception of present-day neuropsychological research on the neural structures of language has resulted in confirming that human language involves parts of the association cortex in the lateral portion of one cerebral hemisphere, usually the left in right-handed individuals. This cortex surrounds the Sylvian fissure and runs from the pars triangularis and opercularis of the inferior frontal gyrus (Brodmann’s area (BA) 45 and 44; Broca’s area) through the angular and supramarginal gyri (BA 39 and 40) and into the superior temporal gyrus (BA 22; Wernicke’s area) in the dominant hemisphere (for reviews, see Caplan, 1987; Gainotti, 1999). Broca and Wernicke regions are crucial for language (Figure 1). Yet the involvement of each area in particular components of language processing is still unknown (Amunts 2008).

Findings from imaging studies confirm the involvement in language processing of the major regions of perisylvian cortex (Broca’s area and Wernicke’s area) identified as the primary language areas on the basis of neuropsychological findings from aphasia study. Both main language areas appear to become active during and to be necessary for language processing, even though neither of them is sufficient for word comprehension or production (Indefrey 2007). A crucially important finding from such research has been that many other cortical and subcortical areas outside the perisylvian language cortex are actively engaged in language processing as well. These structures are not restricted to the language-dominant left hemisphere, but include areas in the nondominant right hemisphere as well. The role of subcortical structures for language and speech is less accessible to study and so are much less well understood than cortical structures, but recent evidence links them closely to cortical mechanisms of language. Some of these structures include the middle and interior sectors of the temporal lobe for its role in word-level processes, the anterior superior temporal gyrus (STG) for its role in the construction of phrases as well as intelligibility, and subcortical structures (basal ganglia and cerebellum) for their role in linguistic computation (Poeppel & Hickok 2004). Recent functional

imaging techniques have also implied the involvement of the premotor cortex in language processing (e.g., Wilson et al., 2004; Skipper et al., 2005). In addition, it has been hypothesized, that the premotor cortex plays a role in the planning but also in semantic processes and categorization (Fadiga et al., 2000; Martin & Chao, 2001). The dorsolateral prefrontal cortex, frontal operculum and the insula participate in different aspects of language processing. The insula has many functions, including integration of limbic and cortical information, and it links anteriorly with the frontal cortex (Trimple, 2007; see Figure 2).

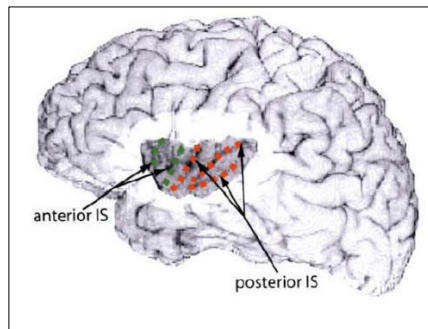


Figure: 2. The position of the left and right insula after portions of the frontal, parietal, and temporal lobes which cover it have been removed. Adapted from Damasio (2005).

The basal ganglia and the thalamus (Figure 3) are subcortical structures that have received the most attention in studies of language processing and subcortical aphasia (Cappa & Abutalebi, 1999; Friederici, 2006). As reviewed by (Kertesz and Wallesch (1993), the basal ganglia are essential relay systems between subcortical and cortical structures. The basal ganglia consist of the striatum, the globus pallidus, and the thalamus. The striatum consists of the putamen and the caudate which are separated by the anterior internal capsule but they are considered to be a unit functionally. The globus pallidus is medial to the putamen and forms the lenticular nucleus with it. The thalamus is the most medial of the nuclei of the basal ganglia, and occupies the two sides of the third ventricle. The thalamus is an important relay station for the ascending sensory and extra-pyramidal motor systems up to the cortex. It receives important input from the cerebellum, the striatum and reach every aspect of the cortex. It has been suggested the basal ganglia is involved in 'rule-based' processing in language, such as regular aspects of word formation. The thalamus may play a role in processing the meanings of words (Caplan, 2009).

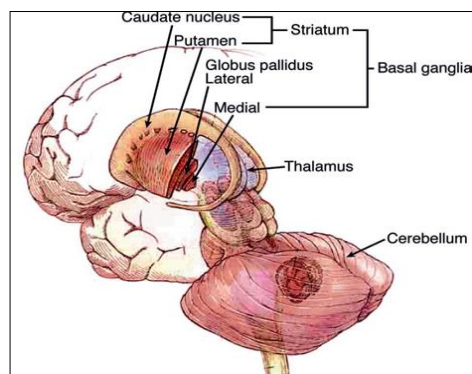


Figure 3: The location of subcortical regions involved in language processing. The insula, a cortical region located deep to the brain's lateral surface at the junction between the frontal,

temporal, and parietal lobes, is not visible in this figure. Adapted from Bornkessel-Schlesewsky & Schlesewsky (2009).

In sum, the findings reviewed have led researchers to consider the importance of brain regions other than the classical language cortex in normal language and aphasia (Bookheimer 2002; Brown & Hagoort 1999; Metter 1995; Patterson & Bly 1999; Poeppel & Hickok, 2004). Consequently, a broader approval of the involvement of the whole brain in language processes have begun to emerge. However, there is still much controversy with respect to its organization in the human brain. The debates today mostly concern how the different functional components of the language system are neuronally instantiated. We address these issues in the following sections.

3. Evidence from Neuropsychological Studies

The initial evidence about how brain supports language functions was gained from investigating the relationship between the observed deficits and the areas of the brain that are affected as a result of injuries such as stroke, head trauma, tumor, or dementia. Observations in two domains, language breakdown and brain lesions, were correlated to describe a coherent account of how brain damage can be expected to affect language performance and how language is organized in the normal brain. The classic aphasia classification traditionally arising from left hemisphere damage that were initially developed in the late 1800s by Wernicke, Broca, and Lichtheim is considered by many to be the most important step in the beginnings of modern aphasiology, and indeed of modern neuropsychology (Tesak & Code, 2008). This scheme, rearticulated during the sixties by Norman Geschwind (1965), constitutes the standard model that has guided research in and out of the neurosciences for almost a century and a half, and its goal is to formulate typologies of language disturbance, using structure-function correlations (Sidtis, 2006). Thus, for example, the left posterior inferior frontal region, Broca's area, was linked to speech production (where brain damage would result in articulatory problems); the left posterior temporal region, Wernicke's area, to auditory speech recognition (where damage would yield impaired language comprehension); and the arcuate fasciculus connecting these anterior and posterior regions to repetition (where damage would impair production by repetition but preserve comprehension). These discoveries were followed by many others that served to accentuate the idea of the modular nature of the brain and the way functions were localized to discrete brain structures (Bookheimer, 2002). Subsequent research has revealed a number of inconsistencies that, on the one hand, cast doubts on such a rigid locationist theory and, on the other hand, provide significant insights into the nature of language representation in the brain. We focus here particularly on the following controversies discussed under the following subsections.

3.1. The Localization Hypothesis: Structure-Function Correlation Principle

One of the major hopes in the investigation of language and its neural correlates has always lain in the assumption that specific language components and/or processes can be associated with particular brain regions. Research into the neural organization of language based on the classical perspective has served to accentuate the idea that major functions of language are primarily localized to the left hemisphere, and that two large brain regions, Broca's area in the posterior portion of the left inferior frontal gyrus (IFG) and Wernicke's area in the left posterior superior temporal gyrus (STG), are crucially involved in language functions (Carter, 1998). This claim has led researchers to speculate that linguistic knowledge is actually embodied in the wiring of these areas of the brain. Specifically, Broca's area is dedicated to grammatical knowledge while lexical knowledge is represented in Wernicke's area. This position upon which the localization hypothesis is built has been challenged on empirical grounds.

First, the results of a number of imaging studies in normal and language-impaired individuals make strong claim against the view that language is located in specific cortical parts of the brain (Broca's area as closely related to speech production while Wernicke's area as associated with speech comprehension), and also confirms the involvement of other neural areas in speech production and comprehension (See critical overviews from different perspectives in Gainotti (1999), Caplan (1996), Grodzinsky (2000), Stowe *et al.* 2005). For example, patients with Wernicke aphasia have difficulty speaking, even if their lesion is restricted to the superior temporal lobe (Pulvermüller, Mohr, Sedat, Hadler, & Rayman, 1996). Similarly, in Broca aphasia, specific comprehension deficits are particularly apparent when patients are confronted with certain sentence types, including, for example, passive sentences (Caramazza & Zurif, 1976). Thus, it would be incorrect to postulate a cortical center specifically for language production and a second independent center processing auditory language input exclusively. Rather, the two areas most crucial for language processing in the cortex, the inferior frontal area of Broca and the superior temporal area of Wernicke, appear to be functionally interdependent (c.f. Pulvermüller 2002; Bornkessel-Schlesewsky and Friederici 2007; Indefrey 2007, for overviews of neuroimaging findings on comprehension and production, respectively), and it has become clear that it is not possible to make a simple distinction between comprehension and production as in the classical model (cf. Hickok and Poeppel, 2000 for a more extensive discussion of the evidence against this distinction).

Second, the classical model has suffered from the assumption that the symptoms of an aphasia are related in a straightforward way to anatomical lesions. There is now a significant body of evidence suggesting that the relationship between function and specific brain region is considerably more complex, and more variable, than was previously believed. For instance, lesions in the frontal and temporal lobes, some of which spared the perisylvian language areas, led to difficulty producing or understanding words. These deficits include problems with words from particular categories – nouns, verbs, or more fine-grained semantic subcategories of words and (Damasio & Tranel, 1993; Humphreys & Forde, 2001). In addition, different lesions around the inferior frontal gyrus correlate with different aphasic symptoms within the overall syndrome of Broca's aphasia (Alexander, Naeser & Palumbo, 1990). This suggests that other areas outside the classical language areas are necessary for unimpaired language processing.

Conversely, damage to the language areas does not always lead to language breakdown. For instance, lesions confined entirely to Broca's area do not lead to a persisting Broca's aphasia, nor do lesions affecting only Wernicke's area lead to a persisting Wernicke's aphasia (Mohr *et al.*, 1978; Dronkers, Redfern, & Knight, 2000). Furthermore, 'one has recognized more negative cases than expected by the classic doctrine on the differential localisation of aphasic syndromes within the left hemisphere' (Poeck, De Bleser, and Von Keyserlingk, 1984: 88). Poeck *et al.* (1984: 85) were led to the conclusion that '[I]ndividual consideration of single patients in groups shows that there is by no means a one-to-one relationship between specific syndromes and particular regions within the language area.' Such findings reveal the limit of anatomically orientated aphasiology by suggesting that not only the effect of "focal" brain lesions is considerably less straightforward than is generally believed, but also that language may rely upon a wide range of cortical and subcortical regions than those classically associated with language function. To use data from pathological conditions in order to claim what is normal is thus connected to great uncertainty. Brown (1977:5) has summarized these problems in the following way:

Given a series of stages in the production of movement A-B-C, a damage in B can either remove function B from the repertoire of performance, block function A or disinhibit function C; a damage in B can also evoke a disturbed function B, allow function A to "overflow" or fail to activate function C. this only concerns the loss

effect of the damage, and a similar set of possibilities apply to the stimulation of B. does the final symptom mirror function A, B or C, the disturbed function of the whole system ABC, or the rest of the brain scans [without] ABC?

Finally, a more general problem of the lesion approach is that for some cognitive functions, alternative brain systems might be available (Hagoort, 2006). In addition, one area within association cortex might be a node in different functional networks (Mesulam, 1998). This implies, on the one hand, that the absence of a cognitive deficit after a lesion to a specific site does not necessarily imply that the lesioned area is not involved in the spared function and, on the other hand, that mapping symptoms to lesions does not presume that the associated brain area is solely responsible for the function in question. Thus in spite of strongly held scientific opinions about the fixed and confined nature of the cerebral representations of language, it should not be surprising that several outstanding voices were raised against the likelihood of such close links between structure and function, especially with regard to language. As a result, a more dynamic notion began to replace the static assumptions: 'The units are not mere independent centers linked by cable pathways. They are, rather, richly interconnected functional regions which form overlapping networks' (Damasio, 1989: 43–44).

3.2. The Modularity Hypothesis: Language Domain-Specificity

The idea that the human mind is composed of faculties or modules realized in specific, dedicated neural architectures is central to the work of the nineteenth -century neurologists. Current linguistic modular views represent a further development of the localizationist perspective with the assumption that language is relatively independent from other cognitive systems and is subserved by a specialized cognitive module (see, for example, Fodor, 1983; Smith and Tsimpli, 1995; Pinker, 1999). A number of examples of selective cognitive disorders that affect specific mental capacities while the rest are left intact have been used to argue for this view of linguistic modularity. For instance, people affected by Specific Language Impairment or genetic dysphasia conserve their cognitive capacities unaltered, but manifest very important linguistic alterations (Newmeyer 1997). Conversely, individuals diagnosed with Williams's syndrome have a mean IQ of 60-70, while their linguistic competence is similar to those of a fully fluent and proficient second-language learner (Bellugi, Marks, Bihrlé, & Sabo, 1993) higher than expected. The striking disparity in the levels of attainment of Williams syndrome individuals in different cognitive domains has been considered to support the view that language may be independent of other mental capacities.

One particularly influential hypothesis that has tended to dominate theoretical discussions of the modularity is the separation between lexical-semantic and grammatical processing observed in certain aphasic patients (e.g., Pinker & Ullman, 1994). The classical distinction between Broca's and Wernicke's aphasia would appear to provide compelling evidence for these claims. According to the traditional characterization of these disorders, patients with Broca's aphasia experience a loss or disruption of grammatical rules resulting from damage to left inferior frontal brain regions; this produces a deficit in syntactic comprehension. By contrast, patients with Wernicke's aphasia experience a loss or disruption in lexical-semantic representations resulting from damage to left posterior temporal brain regions; this produces a deficit in semantic comprehension (Ullman, 2001). This apparent double dissociation suggests the operation of functionally distinct, specialized neural modules for lexical and grammatical representations.

Detailed investigation of the nature of language disorders reveals that the production/comprehension or syntax/semantics dichotomy is not as specific as has been previously suggested, and in fact may be more easily accounted for in terms of a general

processing model. For example, Bates and Goodman (1997), in their paper entitled "On the inseparability of grammar and the lexicon," argue against the autonomy of grammar, and, more generally, against the view that language learning depends on innate abilities that are specific to language. The facts of language breakdown in brain-injured adults, they argue, do not demonstrate a convincing dissociation between grammar and the lexicon, leading them to reject the view that these functions are mediated in the adult by separate, dedicated, domain-specific neural systems (Bates & Goodman, 1999). More recently, Aydelott, kutas and Federmeier (2005) present evidence from some neurophysiological studies demonstrating that language comprehension is subserved by a distributed processing network involving multiple brain areas in both the left and right hemispheres, with no clear distinction between perceptual and conceptual processing. The results presented also demonstrate that the neural mechanisms involved in language comprehension are also responsible for the processing of other kinds of information, including the recognition of visual objects, with no evidence for a discrete, dedicated language system.

Another issue that has tended to dominate theoretical discussions of modularity concerns the isolability of distinct components of the grammar. Under this strong version of the modularity hypothesis it has been postulated that language consists of submodules such as lexical, syntactic, and semantic, which are functionally autonomous, with a restricted domain of analysis and processing (Fodor, 1983; Garrett, 1979). Selective syntactic deficits have been found in aphasic patients where other language abilities are relatively spared (e.g., Berndt & Caramazza, 1980; Caramazza & Zurif, 1976). This has been cited as evidence that the human brain contains a bounded and well-defined faculty or module dedicated exclusively to the representation and/or processing of syntax (Grodzinsky, 1995a, 1995b, 2000; Pinker, 1994). For instance, Grodzinsky (1995, 2000) has claimed that Broca's area '... is neural home to mechanisms involved in the computation of transformational relations between moved phrasal constituents and their extraction sites' (Grodzinsky, 2000: 2).

The results of several large studies of aphasia suggest that there is little evidence to support the view that the organization of the language system itself is modular. In particular, it has been found no systematic relationship between damage to any single brain region and the presence of syntactic comprehension deficits (Caplan, Hildebrandt, & Makris, 1996; Dick *et al.*, 2001; Dronkers *et al.*, 1994). Wernicke's aphasia is said to be primarily a semantic disturbance, but grammatical functions are demonstrably also impaired (Caplan, Waters, DeDe, Michaud, & Reddy, 2004), and phonology is seen as distorted in the non-fluent as well as the fluent aphasias (Levy & Kavé, 1999). Moreover, language impairments in aphasia are not selective with respect to a particular component of the grammar nor do they reflect impairments to particular linguistic representations (Dick *et al.*, 2001). More specifically, aphasic patients' deficits in the processing of grammatical morphemes, are argued not to reflect damage to specific language modules, but rather the sensitivity of these morphological operations to any source of degradation in the global functioning of the relevant brain areas.

These findings from studies of adult aphasia suggest that the relationship between the character of language breakdown and the locus of brain damage is much less straightforward than had previously been believed, and that the deficits revealed seem to have more to do with language processing demands than with abstract linguistic distinctions such as syntax vs. semantics. This interpretation appears to be supported by several studies which show that neurologically intact individuals, including both elderly controls and college students, can be shown to exhibit patterns of linguistic impairment that mirror the various dissociations observed in aphasic patients when required to process spoken utterances under conditions of perceptual and cognitive stress. This is argued to support a distributive model of language in the brain, where

language functions are distributed over several cooperating areas, rather than having any specific locus (Dick *et al.*, 2005).

In addition to the neuropsychological evidence against the modularity view, the issue of language resilience provides another evidence against the modularity perspective of language. There is considerable evidence that cortical tissue is quite plastic in that it can support different representations (Elman *et al.*, 1996). Studies of brain injury have revealed that damage to the left hemisphere which occurs before a critical period is not lifelong, as the right hemisphere can take over the necessary functions. As reviewed by Dick *et al.*, (2005), studies on children with early focal lesions and hemispherectomy tend not to show consistent differences between early left and right hemisphere injury in terms of language abilities. Although these children do tend to show language processing delays relative to their age-matched peers, they show remarkably spared comprehension and production relative to adults with comparable focal lesions. What is more, these results suggest that the usual pattern of brain organization for language—e.g., left hemisphere dominance—is neither inevitable nor even necessary for successful language processing. These findings argue against the notion that language functions are inexorably hard-wired within specific left hemisphere regions; rather, they indicate that the brain has some flexibility to neutrally reorganize such cognitive functions, if necessary.

Finally, within theoretical linguistics, the hypothesis that language consists of submodules or components such as phonological, syntactic, and semantic, which are functionally autonomous, with a restricted domain of processing is controversial. For example, most of linguistic theory posits a logical delimitation between syntax and semantics, which in the past has been intuitively satisfying and useful in language analysis, but which in actual practice does not exist (Sidtis 2006) . These two “levels” commune and interact and signal each other incessantly (Bates & Goodman, 1997; Levelt, 1999; MacDonald, 1993). Further, their status as autonomous, explanatory elements in mental and cerebral processing is not clear. As Geschwind (1974) notes, we cannot expect every nameable feature; e.g., each theoretical linguistic component, to correspond in some obvious way to a particular cortical location. The obvious reason, as stated by Poeppel & Hickok (2004), is that such linguistic components are themselves not monolithic, but have rich internal structure with numerous subcomponents and computational requirements. Therefore, as will be discussed in the next section, it is unlikely that the components of language have a direct instantiation in localized areas of the brain.

4. Evidence from Brain Imaging Studies in Adults

As already mentioned in the introduction, the attempt to associate certain brain regions with language functions has a long and interesting history. Research studying the performance of aphasic patients has yielded a general framework for mapping language functions such as comprehension and production to relatively delimited regions of the left hemisphere (cf. Goodglass & Kaplan, 1972). More recently, with advances in both linguistics and cognitive neuroscience, hypotheses have become much more specific about the neural substrates that support discrete language processes. These lines of work have established that the linguistic computational system – both in terms of its formal organization and real-time processing components – is comprised of many distinct components, such as phonology, syntax, and semantics, that have specialized computational requirements (Poeppel & Hickok, 2004). However, the complexity of neural activation when the brain is engaged in simple language processing tasks as well as the complex nature of the interactions between phonology, semantics, and syntax poses a challenge to the study of these individual processes in language processing. These difficulties have played a significant role in modern functional neuroimaging techniques such as functional magnetic resonance imaging (fMRI), positron emission tomography (PET), and magnetoencephalography (MEG). Thus, much of the research focused on precisely this type of question, namely: Can we identify specific neurocognitive correlates of

the processing of distinct linguistic components? Both PET and fMRI have been extremely useful for identifying brain regions activated in adult language processing.

4.1. Phonetic/Phonological Processing

Traditionally, anterior aphasias with frontal lobe lesions in Brodmann's areas (BA) 44 and 45 have been described as having a deficit in phonological output. Both anterior and posterior aphasias show disturbances in phonological aspects of language input and output (Caplan, 1992). Imaging investigations of speech perception, as reviewed by (Shafer and Garrido-Nag 2007), have identified a number of brain structure–function relationships related to speech perception (Bookheimer, 2002; Scott & Wise, 2004). These include primary auditory cortex (BA 41) and secondary auditory cortex (BA 42). Different portions of these regions are activated in different types of processing. Activation in the bilateral superior temporal gyrus (STG) is observed for pre-lexical processing of phonetic features. The left posterior superior temporal sulcus (STS) shows particular activation for phonetic features and the right STG to melodic variation of speech. Mapping of speech onto lexical-semantic representations activates the left anterior portion of the STS (BA 22). The planum temporale (PT), which is part of Wernicke's area in posterior superior temporal cortex, appears to serve as a motor/sensory interface for any acoustic stimulus. A few studies also suggest that left prefrontal cortex (BA 44/6) is activated in processing rapid transitions, such as those found in consonant–vowel syllables, and in accessing, sequencing, and monitoring phonemes. In summary, the most common cortical areas associated with phonological processing includes posterior brain regions of the superior temporal gyrus (BA 41, 42, 22) for speech perception, and PT for interfacing with the motor system. These regions display somewhat different functions for left versus right hemisphere cortex.

4.2. Semantic/Discourse Processing

The Supramarginal Gyrus (SMG) and angular gyrus regions have been implicated in some aspects of language processing. Though the 19th century language model has described these areas as being specialized for visual word form processing, they are now considered as a part of a more general semantic analysis network (Price, 2000). Moreover, the Inferior Frontal Gyrus (IFG) or the Broca's area has been thought to be specialized for syntactic processing and speech (see Price, 2000, for a review). Neuropsychological studies associate damage to inferior frontal regions, especially BA 44 and 45 (Broca's area) with both syntactic and morphological deficits (Miceli & Caramazza, 1988; Marslen-Wilson & Tyler, 1997,1998; Tyler, 1992). However, in recent neuroimaging studies, the anterior portion of the left IFG has been implicated in processing semantic relationships and/or retrieving semantic information (Poldrack *et al.*, 1999, for a review) and the posterior left IFG (BA 44/45) for syntactical processing (Bookheimer, 2002; Dapretto & Bookheimer, 1999) as well as phonological processing, such as phoneme monitoring or rhyme judgments (Poldrack *et al.*, 1999; Temple *et al.*, 2003). Right cortical regions, typically homologous to the left language regions, are activated in pragmatic/discourse and prosodic functions. These functions include interpreting metaphors and morals, creating coherence, topic maintenance, and using prosody to interpret emotion. For example, right regions, including BA 44/45, dorsolateral prefrontal cortex (BA 46), superior temporal cortex (BA 22), and angular gyrus (BA 39) are highly activated in topic maintenance (Caplan & Dapretto, 2001). Bookheimer (2002) suggested that the right hemisphere activation reflects integration of information over time, whereas left activation during language comprehension indexes interpreting the meaning of individual units. In summary, multiple cortical regions are activated in semantic and discourse processing. The pars orbitalis portion of the inferior frontal

gyrus probably functions in executive control, and activation is sustained throughout processing. Activation of other regions reflects retrieval of the semantic properties of a word. Right hemisphere activation is specifically involved in pragmatic/discourse aspects of processing. In general, imaging work shows lexical representations and meaning based processing broadly distributed in the left hemisphere, with both anterior and posterior regions represented and right hemisphere activation commonly observed.

4.3. Syntactic/Morphosyntactic Processing

Imaging studies show that the pars opercularis in the left third frontal convolution (i.e. in and around Broca's area) is associated with syntactic processing (Caplan, Alpert, & Waters, 1998; Ni *et al.*, 2000; Stromswold, Caplan, Alpert, & Rausch, 1996). The results indicate that parts of Broca's area increase their activity with an increase in syntactic complexity. Recently, however, the role of Broca's area in syntactic processing has been challenged. According to Kaan and Swaab (2002: 355), neuroimaging findings suggests that 'syntactic processing recruits not one brain region but multiple areas that are not each uniquely involved in syntactic tasks'. The authors propose that different parts of the brain may be recruited for different aspects of syntactic processing, such as encoding, storage, and lexical processing (Kaan & Stowe, 2002; Keller, Carpenter, & Just, 2001; Stromswold *et al.*, 1996). In a recent study, Moro (2008) proposes that Broca's area is selectively involved for syntax within a complex net that also involves the activation of subcortical portions of the brain. It is its interaction with the caudate nucleus that constitutes a network that is specifically involved in syntax.

Imaging studies show that processing of morphosyntactic information includes regions in left prefrontal cortex, as shown in Figure 4. The premotor cortex (BA 6), pars opercularis, and putamen (basal ganglia structure) are activated in learning and recognizing simple grammars with phonological encoding, and pars opercularis and triangularis (BA 44/45) are activated in recognizing higher-level grammatical patterns. In posterior cortical regions, the anterior portion of the left superior temporal gyrus is also activated in processing morphosyntactic information (Friederici, 2004; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003). In summary, both imaging and neurophysiological studies indicate that left anterior regions, including Broca's area and basal ganglia subcortical structures, are highly activated in early and late aspects of morphosyntactic processing.

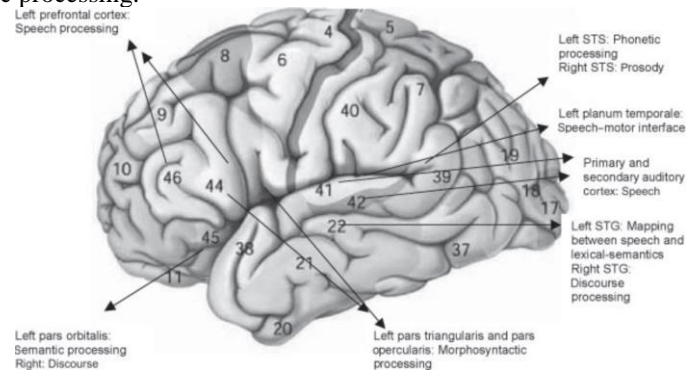


Figure 4: Brain structure–language function relationships. Brain regions typically activated during (1) phonetic/phonological processing related specifically to speech perception, (2) morphosyntactic processing, and (3) semantic/discourse processing. Adapted from Shafer and Garrido-Nag (2007).

To conclude, in spite of indisputable correlations between particular language components and certain neurocognitive processing domains, many recent studies argue against the one-to-one mapping principle between cognitive functions and the activations of a single area and thus challenge the notion that language-related areas subserve language-related functions only. For instance, Saygin, Dick, Wilson, Dronkers, & Bates (2003) point out that to claim a critical role of cortical structures in language processing does not mean that they are uniquely dedicated to language functions. Moreover, research has revealed that one area within association cortex might be a node in different functional networks (Mesulam, 1998). This implies that the appearance of a particular processing effect is not necessarily to claim domain specificity for that area. Conversely, many of the elements of the neural net underlying different aspects of language are also involved in the performance of other cognitive tasks (Kaan & Swaab 2002), in interaction with other brain regions (Heim *et al.* 2003). On this view, a particular cognitive function is most likely served by a wide range of cortical areas, rather than by one local area alone. In addition, a local area participates in more than one function and thus challenge the notion that language-related areas subserve language-related functions only. Consequently, although it is theoretically possible that there is a well-defined cortical region of the brain corresponding to the theoretical linguistic levels, it is just as possible in theory that such a component corresponds to the intersection of several such regions, or even to no anatomically well-defined region, but rather results from the complex interaction of diverse neural networks (Jenkins, 2000). However, this does not mean that many of these regions do not appear to compute specific linguistic representations in particular tasks. It only means that the one-to-one mapping principle between a single anatomical region and a particular cognitive process and vice versa is in many cases not an adequate account of how cognitive functions are neurally instantiated (cf. Hagoort, 2006; Moro, 2008).

Findings from brain imaging studies suggest that language processing activates a complex neural network of primarily left fronto-temporal brain regions in concert with a number of other areas such as the basal ganglia (Bornkessel-Schlesewsky & Schlesewsky 2009). The two most directly involved areas of this Perisylvian network are an inferior frontal region and a superior temporal region, (Broca and Wernicke's areas respectively). These two areas are connected with each other as well as with multiple regions of the temporal, parietal, and frontal lobes (Mesulam, 2010). The precise role of Broca's area in language functioning remains controversial to this day. This issue will be highlighted in the next section

5. Broca's Area and Language Specificity

The influential work of the French neurologist Paul Broca (1861) established that language is a special faculty, instantiated in a specialized neural system primarily involving the left inferior frontal gyrus and posterior temporal cortex (Dronkers *et al.*, 2004). Since its first description in the nineteenth century, Broca's area has represented one of the most challenging areas of the human brain. The first empirical evidence that Broca's area is involved in speech production was provided by Penfield and Roberts (1959). These authors demonstrated that the electrical stimulation of Broca's area in awake neurosurgery patients could evoke a complete arrest of ongoing speech. The hot spot for this effect was located in the pars opercularis of the IFG (Ojemann *et al.*, 1989). Despite some disagreement in the literature on the cortical areas corresponding to Broca's area, most authors agree that Broca's area corresponds to Brodmann's cytoarchitectonic areas 44 and 45 (pars opercularis and pars triangularis of the IFG), although these vary quite considerably in size and location between individuals (Uylings, Malofeeva, Bogolepova, Amunts, & Zilles, 1999). Some publications use the term Broca's area for Bas 44, 45, and 47; others use it for either BA 44 or 45, exclusively.

Recently, the anatomical area and the syndrome named after Broca have both expanded unrecognisably since they were first identified. The emerging position is that the syndrome of Broca's aphasia manifests a nonfluent amalgam of apraxia of speech (or aphemias), speech automatisms, agrammatism, sentence comprehension impairments, deep dyslexia, phonological dyslexia and dysgraphia (Tesak and Code 2008). Moreover, the extent of lesions causing Broca's aphasia is no longer treated as restricted to Broca's area alone. These patients tend to have lesions that include Broca's area (pars triangularis and opercularis of the left third frontal convolution). Several studies have shown, however, that lesions in other brain areas can produce agrammatism, suggesting that other left hemisphere areas can be responsible for this function in some individuals (Vanier & Caplan 1990; Dronkers *et al.* 1994). Mohr *et al.* (1978) found that Broca's aphasia did not result from a lesion limited to Broca's area, but resulted from a large lesion involving the area of supply of the upper division of the left middle-cerebral artery which produces a global aphasia. The damage in Broca aphasia involves cortical tissues which include the operculum, the third frontal convolution, the anterior parietal region, the insula, and both sides of the central Rolandic fissure, as well as the underlying white matter. Dronkers (1996) has shown that lesions to Broca's area are neither necessary nor sufficient for the speech output impairments that define Broca's aphasia. The only region of the brain that seems to be inextricably tied to speech output deficits is an area called the insula, hidden in the folds between the frontal and temporal lobe. This area is crucial, but its contribution may lie at a relatively low level, mediating kinaesthetic feedback from the face and mouth. The fact that Broca's aphasia requires a large lesion that involves multiple brain areas supports the idea that many different regions must participate in the normal processing of language.

A preoccupation of aphasia research has been the role of Broca's area in language. Broca's claim established that the posterior part of the left inferior frontal gyrus (IFG) was of critical importance for speech production. Many functional imaging studies support this claim. For example, studies have shown the involvement of inferior frontal cortex in language production (Kim *et al.*, 1997; Petersen *et al.*, 1988), and in syntactic as well as phonological processing (Friederici *et al.*, 2003; Zatorre *et al.*, 1996). But recent neuroimaging and neuropsychological studies challenge the specificity of the role of Broca's area for language processing and suggest that Broca's area or parts of (Brodmann's area 44) subserves other cognitive functions in addition to speech and hence may be part of human inferior premotor cortex (Binkofski and Buccino, 2004). For instance, several recent experiments have shown that Broca's area seems to be involved in the processing of musical sequences (Koelsch *et al.* 2000; Patel 2003), the imagination of movement (Binkofski *et al.* 2000) and the perception of the rhythm of movement (Schubotz & von Cramon 2003). It has also been argued that listening to complex music and mentally rehearsing music activate much the same areas as language, both Broca's and Wernicke's (Hickok *et al.* (2003).

In addition to the evidence that it is involved in syntactical analysis, mathematical calculation and music processing, Broca's area may play some role in language comprehension. This assumption seems to be supported by several studies demonstrating that Broca's aphasics, in addition to their deficits in production, are also impaired in speech comprehension. Deficits are more evident when patients were tested with verbal material requiring syntactical understanding (Caramazza and Zurif, 1974; Alexander, Naeser & Palumbo, 1990; Caplan *et al.*, 1996). Studies like these led to the development of an alternative view, according to which Broca's area supports syntactic processing in both production and comprehension, while Wernicke's area supports lexical semantic processing (Stowe *et al.* 2005).

However, the key role of Broca's area in syntactic processing has been challenged on the grounds that studies typically involve task and stimulus demands that may activate brain regions that overlap with those involved in linguistic computations, making it difficult to differentiate

between linguistic and non-linguistic processes (Kaan and Swaab, 2002). As reviewed by Stowe *et al.* (2005), recent neuroimaging evidence show that the left inferior frontal gyrus (Broca's area) plays some role in comprehending sentences when processing is more difficult, but combined with the simple sentence results, they suggest that its role is not syntactic processing per se. Most imaging studies show that regions associated with syntactic processing are more circumscribed but nevertheless represented at more than a single cortical region. The conclusion that syntactic processing does not necessarily depend on the left inferior frontal gyrus is also supported by evidence from aphasia, as pointed out in a recent study by Tyler *et al.* (2011). More specifically, in a functional neuroimaging study of the linguistic performance in patients with left hemisphere damage and healthy participants, it has been found that the left inferior frontal gyrus may not itself be specialized for syntactic processing, but plays an essential role in the neural network that carries out syntactic computations. This net involves a variety of brain areas co-activated with the left inferior frontal gyrus, including the right inferior frontal gyrus, bilateral superior temporal gyrus, left middle temporal gyrus and a more posterior temporo-parietal cluster including left inferior parietal lobule, left angular gyrus and left supramarginal gyrus. This suggests that the left inferior frontal gyrus plays an essential role within the neural language network, and that differential modulation within this network underpins different types of linguistic computations Tyler *et al.* (2011).

It is evident that the view that Broca's area is a language-specific area, and therefore it only subserves a specific function, can no longer be held in the light of evidence from recent imaging studies and lesion studies. On this view (argued for vigorously in Hagoort, 2006: 246), 'it would be a serious mistake to assume that Broca's area is a 'language-specific area.' Instead, besides the classical Broca's and Wernicke's areas, several additional distributed cortical and subcortical neuronal structures of both hemispheres clearly make a significant contribution to language function. Imaging and electrophysiological studies have identified an enlarged frontal region engaged in speech and language and Hagoort (2006) has called this enlarged area "Broca's complex," which refers to a series of related but distinct areas in the left prefrontal cortex, at least encompassing BAs 47, 45, and 44 and ventral BA 6. This set of areas subserves more than one function in the language domain and almost certainly other nonlinguistic functions as well. In the context of language processing, activation of this region is seen while experimental participants engage in semantic (BA 47 and 45), syntactic (BA 45, 44, 46) and phonological processing (BA 44, 6). Broca's complex is thus involved in at least three different domains of language processing (semantic, syntactic, phonological), with substantial overlap (see figure 5). As a result, localizing Broca's region in the context of a functional imaging study analyzing linguistic material, or a lesion study of Broca's aphasia may refer to completely different areas with different cytoarchitecture, connectivity and, ultimately, function (Amunts 2008).

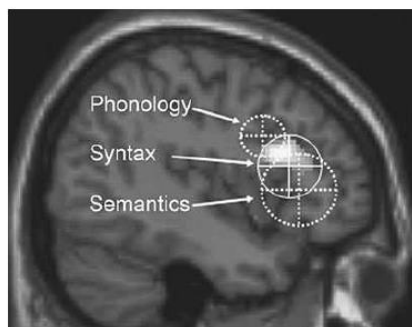


Figure 5: The gradient in left inferior frontal cortex for activations and their distribution, related to semantic, syntactic, and phonological processing. Adapted from Hagoort (2006).

Given the multiplicity of functions associated with Broca's area, a crucial question that arises is: Due to what extent one can claim a functional specificity to Broca's area? According to the prevailing connectionist model (e.g., Pulvermüller 2003), neurons develop billions of connections in a massively parallel network, in which no action or perception could be considered to have a single or simple "impulse." The brain activates many interconnected cortical nodes that are likely to participate in the function of more than one network. In this conception, Broca's area receives its specificity as part of a specialized network. According to Fink et al. (2006) particular neuroanatomical regions, including Broca's area, change their functions consequent upon the simultaneous activation of other regions that are effectively connected to a given region. Hence, context-dependent interactions within networks of areas determine the functions of the constituent areas. This notion of a distributed architecture of brain function suggests that a particular area may be part of different networks and hence its involvement in different functions depends on the input it receives in a given task context.

6. Concluding Remarks

A great deal of progress on brain-language research has been driven by advances in both linguistics and cognitive neuroscience. In particular, research in theoretical linguistics and psycholinguistics has drawn attention to the structure of language processes in unimpaired individuals. These distinct approaches, coupled with the use of functional neuroimaging procedures have confirmed over the basic insights of the classic model, while at the same time extending and complicating the picture of how the hemispheres work in relation to language. Functional imaging findings reveal an array of brain areas involved in language processing, many of which are in conflict with long held assumptions about brain-language relationships. Not only the tradition of linking language-related functions with particular brain regions has been questioned, but a completely new perspective is also being offered. A crucially important finding from such research has been that the brain activates complex neural networks dispersed across both the left and the right hemispheres, even for simpler acts of cognition (Hellige, 2010). So any simple proposal of hemispheric specialization, such as saying that language depends on a relatively small area of the human association cortex situated around the Sylvian fissure, or that a certain brain region, separable from other systems, can be exclusively dedicated to a certain function is implausible.

The same kind of consideration hold with regard to postulation a "language organ/module." In linguistics the view of the brain as a *tabula rasa* for language has led some researchers to speculate that the brain consists of highly specialized language areas and/or circuits. The idea is also central to generative linguistics often taking an explicitly modular and often phrenological position; i.e., the view that the language faculty is a module of the mind separate from other cognitive functions (Chomsky, 1987). Such claims, however, are problematic as they opened the way to unnecessary entailments and to considerable misuse of the ideas that gave linguistics a bad name. Marshall termed this view of linguistics "the new organology" (Marshall, 1980:23). Functional imaging findings suggest that language requires the interaction of numbers of highly integrated systems of the brain. This interaction involves both hemispheres as well as cortical and subcortical structures (Metter, 1995). Moreover, findings in the cognitive electrophysiology of language processing has made it clear that none of the ERP effects discovered to date seems to be unique to language processing. Neuroimaging data clearly suggest that key neural networks dedicated to language functions partially subserves nonlinguistic functions, such as executive system function, working memory, or attention control, which contribute reciprocally

to aspects of language performance (Cahana-Amitay & Albert, 2014). These data therefore do not provide any evidence for the hard-wiring of anything as specific as language. Rather, it suggests a conception of language not a single process but a massively interconnected one; a neural network of cortical and subcortical regions which participate in the performance of other cognitive processes in addition to language. This renewed view of the neural correlates of language is, in fact, consistent with the structural perspective on language as 'a system of interdependent terms in which the value of each term results solely from the simultaneous presence of the others' (Saussure 1959; as quoted in Hudson, 2007). From this point of view, the proposal that there is a mental organ for language that shows autonomy at the levels of knowledge structures and procedures does not necessarily involve the proposition that the neural correlates for such a mental organ refer to discrete neural structures, but rather as a collection of interconnected neuronal pathways whose activation is related to language, with a quite complex topological distribution. Hence, language specialty does not lie in having a dedicated set of cognitive/neural structures to draw upon, but rather in being a cognitive faculty that requires such efficient and intricate coordination of so many domain-general abilities, functions, and information sources (Aydelott, Kutas, Federmeier 2005).

This view of the neural correlates of language lend support to the work of those authors that defend a deeper revision of the traditional localization of language functions and propose that certain subcortical structures are also involved in this faculty. In addition, this new perspective has promoted new models about brain functioning and the neural networks dedicated to language. These new models have largely identified different functional anatomies related to particular word- and/or sentence-level linguistic processes with varying degrees of neural and/or psycholinguistic specificity. For example, Ullman (2004) presents his Declarative-Procedural model, a neurocognitive approach, that is designed to make contact between aspects of language and non-linguistic neural functions such as declarative and procedural memory. In this model, it is proposed that the neural correlates of language consist of two main systems that are, to a certain point, dissociable. One of those systems, related with verbal working memory, declarative memory, or lexical storage, is believed to be supported by a cortically distributed net, not a single localized region. This first system includes Broca and Wernicke's areas, but also their right hemisphere homologues and others in premotor and prefrontal cortices. The second system, related with procedural memory, syntactic rules and other sequencing cognitive operations, involves fronto-striatal circuits, with the basal ganglia, especially the caudate nucleus, constituting a fundamental piece of this net (Ullman 2004: 246).

The concept of dynamic neural networks has challenged the classical assumptions about modularity, domain specificity, and the characterization of language disorders in terms of damage to discrete, language-specific processing modules. In the twenty-first century, researchers know that such a rigid locationist theory is implausible for two reasons: one function involves more than one cortical area and more than one portion of the brain. Conversely the cortical areas and the portions of the brain that are involved can play a role in other functions as well. However, evidence from physiological studies and deficit analysis indicates that the concepts of modularity of language function are useful, provided it is realized that these functions are integrated and participate in more diffusely distributed processes (cf. Kertesz & Wallesch, 1993). Thus, 'it may be that we have to rethink the concept of module and allow for a kind of continuum, from peripheral perceptual systems, which are rigidly encapsulated (not diverted from registering what is out there), through a hierarchy of conceptual modules, with the property of encapsulation diminishing progressively at each level as the interconnections among domain-specific processors increase' (Carston 1997: 20; as quoted in Hudson, 2007:6). This

suggests that a model of brain functioning needs to include both a localization and a distributed processing perspective.

Despite a great deal of progress has been made in understanding the neural mechanisms that underlie language, the problems of relating neural structures and dynamics to specific cognitive functions, including language processes, are many. For instance, when studying the neural correlates of cognitive processes, including language processes, three questions are commonly asked: (i) Where, or in which areas of the brain is a particular process located?; (ii) When, or before and after which other processes, does the particular process occur?, and (iii) How, or by which neuron network type, is the particular process realized? Researchers have spent the last decades focusing mainly on the first question. Indeed, functional imaging techniques have been useful in identifying the areas that become active during a linguistic stimuli as well as in identifying several neural interfaces among language, cognitive, motor, and sensory processes (see Cahana-Amitay & Albert 2014). However, to the best of my knowledge, even the use of such modern research techniques has not definitively answered how and exactly and precisely which cortical-subcortical structures are involved in language functions. A significant challenge has been the manner in which the different elements of the neural networks work and coordinate their activity to execute the complex functions they support (Hellige, 2010). To identify the network of connections throughout the brain that deal with this uniquely human ability and its brain substrates, including the functional contributions of nonlinguistic skills, is a major challenge for the neurosciences in the twenty-first century (Friston, Harrison & Penny, 2003), and successfully dealing with those challenges is likely to lead to a much better understating of the human language system.

Finally, this overview of the current state of knowledge on topics related to brain-language relationships clearly indicates that the field of brain-language search is at the beginning of its growth phase with numerous exciting avenues for future research. There has been extraordinary progress made in recent years in genetics, embryology, and developmental neuroscience. New and important discoveries may come from the use of electrophysiological techniques such as transcranial magnetic stimulation (TMS) or evoked potentials. (For a review of these techniques, see Calvin and Ojemann 1994.) Finally, in vivo brain investigation makes use of a combination of neuroradiology and computer science in order to produce investigative techniques such fMRI or PET. Research using these techniques is likely to continue to change our ideas of the way the human brain supports language functions. One important aspect of this enterprise is that it is truly multi-disciplinary, involving cooperation between linguistics, psychology, genetics, neuroanatomy and other related disciplines.

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