

Neurolinguistics

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<https://doi.org/10.36505/ExLing-2006/01/0002/000002>

Abstract

Neurolinguistics studies the relation of language processes to the brain. It is well established that the critical brain regions for language include the perisylvian association cortex, lateralized to the left in most right-handed individuals. It is becoming increasingly clear that other brain regions are part of one or more complex systems that support language operations. Evidence regarding the more detailed organization of the brain for specific language operations is accruing rapidly, due to functional neuroimaging, but has not clearly established whether specific language operations are invariantly localized, distributed over large areas, or show individual differences in their neural substrate.

Introduction

“Neurolinguistics” refers to the study of how the brain is organized to support language. It focuses on the neural basis of the largely unconscious normal processes of speaking, understanding spoken language, reading and writing.

Data bearing on language-brain relations come from two sources. The first are correlations of lesions with deficits, using autopsy material, magnetic resonance imaging (MRI), positron emission tomography (PET), direct cortical stimulation, subdural stimulation, and transcranial magnetic stimulation. The logic of the approach is that the damaged areas of the brain are necessary to carry out the operations that are deficient at the time of testing, and undamaged areas of the brain are sufficient to carry out intact operations. The second source of information is to record physiological and vascular responses to language processing in normal individuals, using event related potentials (ERPs), magnetoencephalography (MEG), cellular responses, positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). The logic behind this approach is that differences in the neural variable associated with the comparison of performance on two tasks can be related to the operation that differs in the two tasks. This approach provides evidence regarding the brain areas that sufficient to accomplish the operation under study. Functional neuroimaging studies in patients can reveal brain areas that are sufficient for the accomplishment of an operation that were not active prior to damage to the areas that usually support an operation.

The Gross Functional Neuroanatomy of Language

Beginning in the late nineteenth century, the application of deficit-lesion correlations based on autopsy material to the problem of the regional specialization of the brain for language yielded the important finding that human language requires 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 areas (BA) 45, 44: Broca's area), through the angular and supramarginal gyri (BA 39 and 40) into the superior temporal gyrus (BA22: Wernicke's area) in the dominant hemisphere (Fig 1). For the most part, the connections of these cortical areas are to one another and to dorsolateral prefrontal cortex, lateral inferior temporal cortex, and inferior parietal lobe. These regions have only indirect connections to limbic structures (Geschwind, 1965). These areas consist of many different types of association cortex.



Figure 1. A depiction of the left hemisphere of the brain showing the main language areas.

Data from other sources – deficit-lesion correlations based on ante-mortem neuroimaging, functional neuroimaging – has provided evidence that regions outside the perisylvian association cortex also support language processing. These include the inferior and anterior temporal lobe, the supplementary motor cortex, subcortical nuclei such as the thalamus and striatum, the cingulate gyrus, and the cerebellum. Whether these areas are responsible for the computations of the language processing system or only support cortical areas in which these computations occur remains under study. These areas are connected by white matter tracts, in which lesions can produce language disorders.

The statistics regarding gross hemispheric dominance for language are now quite well established. In about 98% of right-handed individuals, the left hemisphere is dominant. About 60% - 65% of non-right-handed individuals are left-hemisphere dominant; about 15% - 20% are right-hemisphere dominant; and the remainder appear to use both hemispheres for language processing (Goodglass and Quadfasel, 1954). The relationship of dominance for language to handedness suggests a common determination of both, probably in large part genetic (Annett, 1985). The neural basis for lateralization was first suggested by Geschwind and Levitsky (1968), who discovered that part of the language zone (the planum temporale -- a portion of the superior temporal) was larger in the left than in the right hemisphere. Subsequent studies have confirmed this finding, and identified specific cytoarchitecturally defined regions in this posterior language area that show this asymmetry (Geschwind and Galaburda, 1987). Several other asymmetries that may be related to lateralization have been identified although the exact relationship between size and function is not known. The "nondominant" hemisphere is involved in many language operations, such as representing word meanings, and some language operations may be carried out primarily in the right hemisphere (e.g., revising inferences, interpreting non-literal language, and appreciating humor).

In summary, a large number of brain regions are involved in representing and processing language. The most important of the regions used to support the normal production and comprehension of literal propositional language appears to be the dominant perisylvian cortex. Ultimately, all areas interact with one another as well as with other brain areas involved in using the products of language processing to accomplish tasks. In this sense, all these areas are part of a "neural system" for language, but there is evidence, reviewed below, that many of these areas compute specific linguistic representations in particular tasks.

Models of Organization of the Brain for Language Processing

Two general models of the relationship of areas of the brain to components of the language processing system have been developed. Localizationist theories maintain that language processing components are localized in specific parts of the brain. "Holistic" theories maintain that linguistic representations and processes require broad areas of the brain. Five basic models, which capture the set of logically possible relations of brain areas to language processes, can be extracted from these two conceptualizations: invariant localization, variable localization, even distribution, invariant uneven distribution, and variable uneven distribution.

Invariant localization hypothesizes that only a small area of the brain supports a function. Variable localization hypothesizes that different small areas of the brain support a function in different individuals. Distribution hypothesizes that a large region of the brain supports a function. Traditional distributed models (e.g., Lashley, 1950, modelled by Wood, 1978) assumed an even distribution of distributed functions: all parts of the region contributed equally to the function. If a function is evenly distributed throughout a region, there can be no individual variability in its neural basis. If a function is unevenly distributed throughout a region, it may be distributed the same way in everyone (invariant uneven distribution) or differently in different individuals (variable uneven distribution). Other models are extensions of these basic five. Degeneracy is a variant of localization in which more than one structure independently supports a function (Noppeney et al, 2004); degeneracy can either be invariant (the same areas independently support the function in everyone) or variable (different areas independently support the function in different people). Variable localization could be constrained so that a function is localized more often in one area than another.

It is not possible to review all the areas of language whose neurological basis has been studied. I shall review work on comprehension at the lexical and syntactic levels, highlighting new concepts and examining the evidence that supports them.

Lexical Access and Word Meaning

Evidence from normal and impaired human subjects suggests that temporospectral acoustic cues to feature identity appear to be integrated in unimodal auditory association cortex lying along the superior temporal sulcus immediately adjacent to the primary auditory koniocortex (Binder, 2000). Some researchers have suggested that the unconscious, automatic activation of features and phonemes as a stage in word recognition under normal conditions occurs bilaterally, and that the dominant hemisphere is the sole site only of phonemic processing that is associated with controlled processes such as subvocal rehearsal and conscious processes such as explicit phoneme discrimination and identification, making judgments about rhyme, and other similar functions.

Based on functional neuroimaging results, activation of the long term representations of the sound patterns of words is thought to occur in the left superior temporal gyrus. Scott and her colleagues have argued that there is a pathway along this gyrus and the corresponding left superior temporal sulcus such that word recognition occurs in a region anterior and inferior to primary auditory cortex, and that word meanings are activated further along this pathway in anterior inferior temporal lobe bilaterally (Scott and Wise, 2004).

This pathway constitutes the auditory counterpart to the visual “what” pathway in the inferior occipital-temporal lobe.

Speech perception is connected to speech production, especially during language acquisition when imitation is crucial for the development of the child’s sound inventory and lexicon. On the basis of lesions in patients with repetition disorders known as “Conduction aphasia,” the neural substrate for this connection has been thought to consist of the arcuate fibers of the inferior longitudinal fasciculus, which connect auditory association cortex (Wernicke’s area in the posterior part of the superior temporal gyrus) to motor association cortex (Broca’s area in the posterior part of the inferior frontal gyrus). Recent functional neuroimaging studies and neural models have partially confirmed these ideas, providing evidence that integrated perceptual-motor processing of speech sounds and words makes use of a “dorsal” pathway separate from that involved in word recognition (Hickok and Poeppel, 2004).

Traditional neurological models maintained that the meanings of words consist of sets of neural correlates of the physical properties that are associated with a heard word, all converging in the inferior parietal lobe. It is now known that most lesions in the inferior parietal lobe do not affect word meaning and functional neuroimaging studies designed to require word meaning do not tend to activate this region. Evidence is accruing that the associations of words include “retroactivation” of neural patterns back to unimodal motor and sensory association cortex (Damasio, 1989), and that different types of words activate different cortical regions. Verbs are more likely to activate frontal cortex, and nouns temporal cortex for nouns, possibly because verbs refer to actions and nouns refer to static items. A more fine-grained set of distinctions has been made within the class of objects themselves. Both deficits and functional activation studies have suggested that there are unique neural loci for the representation of categories such as tools (frontal association cortex and middle temporal lobe), animals and foods (inferior temporal lobe and superior temporal sulcus), and faces (fusiform gyrus) (see Caramazza and Mahon, 2006, for review). Debate continues as to whether such divisions reflect different co-occurrences of properties of objects within these classes, or possibly innate human capacities to divide the world along these lines. At the same time as these specialization receive support, evidence from patients with semantic dementia and from functional neuroimaging indicates that a critical part of the semantic network that relates word meanings and concepts to one another is located in the anterior inferior temporal lobes.

Syntactic Comprehension

Syntactic structures determine the relationships between words that allow sentences to convey propositional information – information about thematic roles (who is initiating an action, who receiving it, etc.), attribution of modification (which adjectives are assigned to which nouns), scope of quantification, co-reference, and other relations between words. The propositional content of a sentence conveys a great deal of information beyond what is conveyed by words alone, and is crucial to many human intellectual functions. Propositions are the source of much of the information stored in semantic memory. Because propositions can be true or false, they can be used in thinking logically. They serve the purpose of planning actions. They are the basic building blocks of much of what is conveyed in a discourse.

Unlike models of the neural basis for lexical access and lexical semantic processes, a variety of models have been proposed regarding the neural basis for syntactic processing, ranging from localization, though distribution to variable localization.

Evidence supporting these models based on correlating deficits in syntactic comprehension to lesions is limited, both in terms of psycholinguistic and neural observations. Many patients have only been tested on one task, and we have found that there is virtually no consistency of individual patients' performances across tasks, raising questions about whether it is correct to say that a patient who fails on a particular structure in a single task has a parsing deficit. Lesions have usually not been analyzed quantitatively and related to performance using multivariate statistics.

We have just reported the most detailed study of patients with lesions whose syntactic comprehension has been assessed (Caplan et al, in press). We studied forty-two patients with aphasia secondary to left hemisphere strokes and twenty-five control subjects for the ability to assign and interpret three syntactic structures in enactment, sentence-picture matching and grammaticality judgment tasks. We obtained magnetic resonance (MR) and five-deoxyglucose positron emission tomography (FDG PET) data on 31 patients and 12 controls. The percent of selected regions of interest that was lesioned on MR and the mean normalized PET counts per voxel in regions of interest were calculated. In regression analyses, lesion measures in both perisylvian and non-perisylvian regions of interest predicted performance after factors such as age, time since stroke, and total lesion volume had been entered into the equations. Patients who performed at similar levels behaviorally had lesions of very different sizes, and patients with equivalent lesion sizes varied greatly in their level of performance. The data are consistent with a model in which the neural tissue that is responsible for the operations underlying sentence comprehension and syntactic processing is localized in different neural regions, possibly varying in different individuals.

Functional neuroimaging studies have led many researchers to articulate models in which one or another aspect of parsing or interpretation is localized in Broca's area, or in portions of this region, and some researchers have argued that "Universal Grammar," in Chomsky's sense (the innate capacity that underlies the ability to acquire the syntax of natural language) is localized in this region. However, most neuroimaging studies actually show that multiple cortical areas are activated in tasks that involve syntactic processing. Overall, the data are inconsistent with invariant localization, and suggest variation in the localization of the areas that are sufficient to support syntactic processing within the language area across the adult population, with perhaps some constraint on the areas in which processing is localized as a function of how proficient individuals are at assigning syntactic structure and determining the meaning of sentences (Caplan et al, 2003).

Final Notes

Human language is a unique representational system that relates aspects of meaning to many types of forms (e.g., phonemes, lexical items, syntax), each with its own complex structure. Deficit-lesion correlations and neuroimaging studies are beginning to provide data about the neural structures involved in human language. It appears that many areas of the brain are either necessary or sufficient for representing and processing language, the left perisylvian association cortex being the most important such region. How these areas act to support particular language operations is not yet understood. There is evidence for both localization of some functions in specific regions and either multi-focal or distributed involvement of brain areas in others. It may be that some higher-level principles operate in this area, such that content-addressable activation and associative operations are invariantly localized and computational operations are not, but many aspects of these topics remain to be studied with tools of modern cognitive neuroscience.

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