Cognitive Neuroscience
Language

Language is a form of communication that is unique to the human species. Other animal species communicate, but not by any means remotely close to human language.

Since the time of Broca and Wernicke, it has been thought that language is the product of the two portions of the left human cerebral cortex that bear their names: Broca’s area for language production and Wernicke’s area for language comprehension. Recent studies have raised questions about whether:
1) other areas may also belong to a “language network”
2) Broca’s and Wernicke’s areas subserve only language function

There is no reason to believe that language has a cortical basis that is different from other cognitive functions. For example, there does not appear to be any specialized language module having unique neuronal circuitry. Furthermore, linguistic function is not possible without support from the other cognitive functions of perception, action, memory, and attention. There is good reason to believe that linguistic function rests on the same type of transactions, within and between cortical memory networks, which support those other cognitive functions. Therefore, we should consider language as a function of the entire cortex.
Neurobiology of language

In human prehistory, language appears to have emerged gradually, with speech preceding writing. On an evolutionary time scale, however, its appearance was sudden. Prior to the prehistoric onset of language, human society possessed a system of non-linguistic cognitive communication – based on sounds and gestures.

Language complemented the repertoire of non-linguistic expression possessed by humans (and many other mammalian species) to adapt the human species to its environments.

By comparative studies of different species, differences can be seen in the degree of communication among conspecifics:

1) Animals such as the salamander have minimal conspecific communication.
2) Communication is greater in animals with more developed brains such as primates.
There are corresponding differences in brain anatomy:

1) The salamander brain lacks layered cortex. The forebrain of each hemisphere is a mass of neuropil that contains prototypical functional subdivisions. However, they are not defined by differences in lamination, as in the mammal, but only by connectivity.

2) By comparison, the primate brain has greater development and expansion of:
   a) the limbic system, including orbitofrontal cortex and cingulate cortex
   b) lateral neocortex

   a) Expansion and elaboration of the limbic regions provides the primate with the ability to communicate instinctively and emotionally with conspecifics.

   b) Expansion and elaboration of the lateral neocortex further provides the primate with the cognitive substrate of language.
Limbic basis of primate communication:
The dependency of communication on limbic structures implies that:
1) language is heavily influenced by internal drives and emotional states
2) strong emotion can dominate language – this is evidenced by:
   a. the subcorticalization of language after massive cortical damage, in which speech is reduced to primitive emotional expression
   b. explosive vocalizations in Tourette’s syndrome and obsessive-compulsive disorder (OCD) – perhaps caused by abnormal intrusions into neocortical cognition by limbic areas
3) vocal communication in nonhuman primates is controlled by limbic structures

Lateral neocortex basis of primate communication:
Development of the neocortex in the great apes allows only limited symbolic communication. They can learn rudimentary sign language to symbolize nouns and actions, but they do not learn syntax.

*Linguistic syntax* in humans is closely correlated with the *syntax of action* – the capacity for complex motor sequencing. They both depend on the left frontal lobe.
The associative cortices of the temporal, parietal, and occipital lobes process the semantic aspects of language, whereas the associative cortex of the frontal lobe processes the productive aspects.

In the human species, there is a large increase in the numbers of neurons and of their connections in the associative areas in comparison to other species. This is accompanied by a large increase in subcortical white matter, largely composed of long-range fiber pathways connecting cortical areas.

In individual human development, these areas are the latest to mature in axon myelination, and dendritic branching.

The same huge expansion in connectivity of association cortex that supports human nonlinguistic cognitive function also supports language.

The same combinatorial power of that connectivity that explains the astronomical number of individual cognitive memory networks and memories that can be made also explains the creative potential of language.
A longstanding debate on language concerns the degree to which language is determined by genetics and that to which it depends on upbringing (or experience). It is sometimes called the nature-versus-nurture debate.

According to Chomsky, language is genetically inherited, and furthermore is the foundation of all cognition.

It is an empirical fact that most children rapidly and easily acquire the structural rules for language. These rules allow children to form new and meaningful phrases and sentences. By age 10, most children have learned these rules of syntax, along with phonetics, vocabulary, and prosody of their native language.

In Chomsky’s theory, children have an innate instinct for the grammatical structure of language. They express what he calls a universal grammar. Language involves the creation of grammatical structures of meaning according to rules that do not need to be taught to the child.

There may be a phyletic memory for grammatical structure in the cortex that provides the child with these rules.
In learning language, children learn:
1. a large vocabulary
2. a large set of associations between words and objects; between objects; and between words
3. to categorize words and objects
4. associations between words and objects with affects and needs
5. to use words and manipulate objects to satisfy their needs

To learn these semantic and conceptual associations requires synaptic plasticity to link neuronal assemblies at the highest levels of association cortex.

A connective framework in association cortex to support associations of meaning may be genetically determined and available from birth.

Thus, there may be an innate cortical network structure for learning the rules of grammar.
Hemispheric lateralization

The development of language in children correlates with the development of motor skills. Many of the same skills that allow one to organize behavioral sequences also allow one to organize spoken language.

It has been suggested that motor coordination, like language, is left-hemisphere dominant. The idea is that Broca’s area may be the homologue of a phylogenetically older left-frontal region specialized for object manipulation.

In ontogeny, the child’s ability to manipulate objects in a purposive manner develops at around the same time as the ability to articulate meaningful sequences of words. Presumably both abilities depend on development of the same left-frontal cortical region.

Damage to the cortex of the left hemisphere of the human brain often leads to language impairment (aphasia). However, the neural system for language is plastic – it is often able to recover lost function over time and rehabilitation.

Recovery of function often occurs when other cortical or subcortical regions take over the lost ability.

The right hemisphere can take over language function (partially or completely) if the left hemisphere is damaged early in life.
It is not known why the left hemisphere is dominant for language.

It has been proposed that there is a left dominance for the control of communication from the metencephalon up to the telencephalon, i.e. throughout the brain.

The dominance may be related to lateralization in the distribution of the ascending neurotransmitter systems.

Left dominance does not result from left hemisphere maturing more rapidly before birth. However, the left hemisphere is already specialized for different perceptual and motor functions at an early post-natal age.

**Dichotic listening studies:** children younger than 3 months show a right-ear (left hemisphere) advantage for phonetic discrimination and a left-ear (right hemisphere) advantage for music discrimination.

Neonates also have a greater tendency to turn to the right (contralateral to the left hemisphere) either spontaneously or in response to sensory stimuli. This tendency strongly correlates with right-handedness later in life.
Norman Geschwind studied anatomical asymmetry in the adult brain. He found that in most human adult brains, an area of cortex in the posterior wall of the Sylvian fissure (lateral sulcus), called the planum temporale, is larger on the left side than the right.

This region contains the posterior language area, which includes Wernicke’s area (Brodmann area 22).

Structural MRI studies show anatomical asymmetry in the posterior language area, and also the anterior language area, containing Broca’s area (Brodmann areas 44,45).

These anatomical asymmetries are correlated with right-handedness (left hemisphere motor dominance) and left hemisphere language dominance.

In an fMRI study of language, Binder et al (1997) showed strong left lateralization, with language-related activity extending beyond Wernicke’s and Broca’s areas to other frontal, temporal, and parietal cortical areas, as well as left-sided subcortical structures (but the cerebellum on the right side). There was also activation of right-hemisphere cortex.
Studies by George Ojemann show that direct electrical stimulation of the exposed cortex in awake human patients can selectively and reversibly block linguistic operations, specifically the naming and recognition of lexical entities. From such electrical stimulation studies, we now know that:

a) There is a large region of left-hemisphere cortex in each patient having language function.
b) This region usually includes Wernicke’s and Broca’s areas, but also extends outside of these classical language areas.
c) There is large variability from subject to subject in the region of left-hemisphere cortex that shows language function.
d) Perception, attention, memory affect recognition & naming of lexical entities.
Conclusions about language from lesion, imaging and stimulation studies

a) Language function is dominated by a large-scale cortical network in the left hemisphere.
b) This network has nodes in the classical language areas, but also outside of them.
c) The spatial extent (topography) of the network varies considerably from one person to another.
d) This network interacts with perceptual and conceptual memory networks, and the overall activation of these networks is subject to modulation by attention and working memory, giving language access to sensory inputs, as well as long-term perceptual and executive memories.
e) The specific patterns of activation of these networks are dependent on the cognitive content of language and the cognitive operations necessary to comprehend and express language.
Evidence from bilingual subjects

After extensive left hemisphere damage, bilingual people usually lose both languages. They often experience recovery of function:
1) Some patients recover both languages in parallel.
2) Others recover one before the other.
3) Others recover the languages in steps with temporal alternation.
4) The native or most practiced language usually shows preferential recovery (this may be due to factors affecting relearning rather than representation differences in the brain).

The Wada test shows that both languages are usually lateralized to the left hemisphere. Ojemann’s cortical stimulation studies confirm this, and also show that they have different but overlapping spatial topographies.
Other evidence

Sign language is represented as other languages in the dominant hemisphere, but has a greater degree of bilateral representation than spoken language.

Music, which may be considered a type of language, appears to be hemispherically lateralized.

a) Musical abilities such as recognition of melodies have been localized to the superior & middle temporal gyri of the right hemisphere by the Wada test and lesion studies.

b) More analytic musical abilities are localized to the left (or dominant) hemisphere.

E.g. MEG studies show pitch discrimination localized to the left auditory cortex in experienced musicians.

Also, neuroimaging studies show activation of cortex near Wernicke’s area in musical sight-reading, and activation of cortex near Broca’s areas in musical keyboard performance.
Neuropsychology of language

Aphasia is any disorder of language. It typically results from lesion of the cortex.

A. Wernicke’s aphasia: a disorder of the semantics of language
   1. results from lesion in posterior superior temporal lobe
   2. difficulty comprehending word meaning
   3. no difficulty articulating language, i.e. speaking
   4. patient may engage in profuse & illogical speech production
   5. described as sensory or fluent aphasia

B. Broca’s aphasia: a disorder of the articulation of language
   1. results from lesion in posterior lateral frontal lobe & frontal operculum
   2. no difficulty comprehending word meaning
   3. difficulty articulating words and sentences
   4. absence of function words (articles, pronouns, conjunctions, prepositions)
      – speech sounds telegraphic and agrammatical
   5. described as motor or nonfluent aphasia
C. **Global aphasia**: a disorder displaying symptoms of both Wernicke’s and Broca’s aphasias
   1. results from lesion that affects both posterior and frontal language regions
   2. almost total reduction of all aspects of spoken and written language
   3. patients often mute
   4. non-linguistic cognitive skills intact

D. **Conduction (transcortical) aphasia**: a disorder displaying mixed symptoms
   1. classically thought to be due to disconnection of Wernicke’s and Broca’s areas; this interpretation has been questioned
   2. intact auditory comprehension
   3. fluent speech
   4. poor speech repetition
Lichtheim’s model

*Lichtheim* published a treatise on aphasia in 1885. In his model, spoken language enters the acoustic center (A), which projects to a motor center (M) and also to one or more conceptual centers (B’s).

We no longer speak of brain “centers”. However, the conceptual centers are seen to correspond to the frontal and posterior cortical association areas, substrates for high-level executive and perceptual memory networks.
The acoustic center may correspond to the posterior language region, including Wernicke’s area, and also the *angular gyrus* (Brodmann area 39).

![Brain diagram](image)

The angular gyrus (39) is the parietal area colored orange. It is posterior to Wernicke’s area (22 - green) and the supramarginal gyrus (40 - yellow).

Geschwind proposed that the angular gyrus is where the written word is translated to internal monologue.

Both the angular gyrus and the supramarginal gyrus may be involved with non-auditory aspects of language comprehension.
Difference between Wernicke’s and Broca’s areas in hierarchical level

Wernicke’s area lies high in the perceptual hierarchy, above unimodal association cortex.
Broca’s area lies relatively low in the executive hierarchy, in premotor cortex.

Implications:
  1. Lesions of Wernicke’s area sometimes cause deficits in conceptual functions as well as language comprehension.
  2. Frontal regions higher in the executive hierarchy than Broca’s area may play a role in the executive control of language expression.
Lesions of the posterior language region outside of Wernicke’s area

Lesions of the posterior language region, but not in Wernicke’s area (outside Brodmann area 22 of the dominant hemisphere), can produce a deficit of recognition of structured language – called (semantic associative) agnosia. *Semantic associative agnosia* is lack of recognition of words & sentences. (The distinction between discriminative and associative agnosia derives from Lissauer, 1890, who distinguished “apperceptive” and “associative” agnosias.)

Lesions in higher levels of association cortex (in posterior language region but outside of BA22) affect “linguistic manifestations” of higher-order perceptual memory networks:

1. inability to name visually presented objects – implies impairment of cross-modal (visual-auditory) memory networks
2. inability to understand written language – implies impairment of lexical memory networks (vocabulary knowledge)
3. inability to identify object categories – implies impairment of categorical memory networks (e.g., loss of ability to distinguish animate from inanimate objects, or fruits from vegetables)

**Conclusion about linguistic comprehension:** the network hierarchies for perceptual memory also serve as the semantic substrate for language.
Posterior memory network hierarchy for semantic substrate of language

1) The lowest level of the network hierarchy for language is in auditory association cortex (BA 42): *phonological* memory networks are formed by vocal sound (phoneme) association.

2) At middle levels, transmodal memory networks are formed by association of phonemes with perceptual entities from other modalities, especially visual (written) words.

3) At the highest levels, other transmodal memory networks are formed by categorical and conceptual associations. The word sounds associated with categories and concepts may be organized in parallel lexical networks.
**Linguistic Production**

The network hierarchies for action and executive memory also serve as the productive substrate for language.

Frontal memory network hierarchy for productive substrate of language

1) The lowest level is the primary motor cortex for the speech musculature.

2) Above this level is premotor cortex (BA6), containing memory networks for simple propositions and elementary syntactic structure. Specially important is the SMA of the dominant hemisphere – lesions here produce motor aphasias similar to Broca’s aphasia but with less disruption of syntax & grammar.

3) At the highest level:
   a) medial prefrontal cortex, especially anterior cingulate cortex (ACC): lesions may impede speech, and even cause mutism if large enough. May be due to loss of attentional and motivational drive to language production.
   b) lateral prefrontal cortex: lesion may produce central motor aphasia (or frontal dynamic aphasia) – characterized by: (i) low speech fluidity & spontaneity; and (ii) impoverished linguistic structure – lack of ability to conceptualize, plan, and execute complex linguistic structures.
Double dissociation of linguistic categories in frontal & posterior regions

Evidence suggests that verbs and other action words are represented in left lateral frontal cortex, whereas nouns and object names are represented in left posterior association cortex. A focal region for noun representation in left superior temporal cortex extends into the angular gyrus – the region proposed to be involved in naming by Geschwind.

This dissociation is supported by careful study of clinical lesion effects. However, it is also seen by stimulation studies. The production of verbs and nouns is disrupted by TMS applied to one or the other region of the left hemisphere.
Functional architecture of semantics

Semantics refers to the “meaning” of language. Symbolic units of meaning are called words. The meaning of most words is arbitrary – it does not derive from phonic similarity to sounds.

The hierarchy of semantic content extends from words that symbolize concrete entities, to those that symbolize classes of entities, classes of classes of entities, to those symbolizing abstract concepts. Neurophysiological correlates of semantics in the cerebral cortex have been found through the study of: (A) ERPs; (B) neuroimaging; (C) language development; and (D) dyslexia.

A. ERP results

Event-Related Potential (ERP) studies of language support the evidence from other techniques.

ERP amplitude differences have been reported in response to word stimuli of different semantic categories, depending on the brain region where the ERP is recorded.
1. Verbs vs nouns

Some ERP evidence suggests a distinction between frontal and posterior language representation of nouns and verbs.

Verbs elicit larger ERP components than nouns at frontal locations. Nouns elicit larger ERP components than verbs at posterior (parietal, temporal, occipital) locations.

These amplitude differences occur mainly in late ERP components, i.e. longer than 200 msec after stimulus onset.

2. OC words vs CC words

Other ERP studies suggest that a distinguishing feature between frontal and posterior language representation is between open- and closed-class words.

Open-Class (OC) words: content words such as nouns, verbs, adjectives
Closed-Class (CC) words: function words such as articles, pronouns, prepositions, conjunctions
In one study (Neville et al. 1992):
OC words were found to elicit a negative potential at 350 ms post-stimulus, largest at posterior (parietal, temporal, occipital) locations.
CC words were found to elicit a negative potential at 280 ms post-stimulus, largest at frontal locations.

This result is consistent with a distinction between the role of frontal cortex in the syntax of language and the role of posterior cortex in the semantic content of language.

The posterior localization of semantic processing is supported by many other ERP studies, e.g. those on the N400.

The N400 ERP component is typically elicited when an incongruous word occurs out of linguistic context in a sentence, e.g. I take coffee with cream and dog. Anomalous content words, that violate semantic congruity, elicit a late (~400 ms), long-lasting negative potential at posterior locations. This does not occur for function words that violate syntactic congruity.
B. Neuroimaging results

Neuroimaging refers to the functional mapping of “activation” patterns using PET or fMRI. Neuroimaging may be performed while subjects perform a language task.

Cabeza & Nyberg (2000) performed a meta-analysis of the neuroimaging literature on language. Their results are shown as maps of the lateral and medial surfaces of both hemispheres, with a peak activation mark for each study.

These meta-activation maps show concentrations of peak activations largely in the peri-sylvian cortex of the left hemisphere for language function.

1) The areas activated by spoken and written words largely overlap.
2) Written words activate visual occipital areas in addition to language areas.
3) Access to the meaning of words involves the anterior language production areas.
4) The cerebellum is also involved in language function – probably as part of the executive system that controls the orderly execution of all purposeful actions, including language production.
Neville et al (1998) studied fMRI in 3 groups of subjects:
1) normal hearing monolinguistic English speakers
2) deaf people who use American Sign Language (ASL) as their native language and know English as a second language
3) bilinguals for whom ASL and English are both native languages, i.e. hearing native signers

Comprehension of both English & ASL involves strong activation of classical language areas in native speakers of those languages.

They also involve activation of non-classical regions:
1) angular gyrus
2) anterior & middle superior temporal cortex
3) dorsolateral prefrontal areas

Interpretation of these results:
1) The two languages develop the cognitive substrate for language in the left hemisphere early in life.
2) With experience, that substrate grows to include associative cortical areas of the left hemisphere – the semantic memory networks in these areas becoming multimodal and heterarchical.
3) The learning of ASL by signers recruits areas of both hemispheres for processing the visual & motor information needed by this language, and this processing recruits additional memory networks.
C. Development of language

Babbling is the spontaneous production of speech sounds by the infant child without production of recognizable words. Babbling emerges at age 5-7 months when the infant’s vocalizations begin to sound like phonemes. At ~12 months, recognizable words usually appear.

1. Since babbling is innate, and appears to depend on the left peri-sylvian regions, it is likely that the connective architecture of these areas is genetically determined.

2. Building on the rudimentary architecture present at birth, it is likely that experience drives the formation of memory networks to first represent syllables, then words, and then syntax in surrounding non-classical areas.

3. With continuing experience, the memory networks built around the core language areas become associated with memory networks of the higher frontal & posterior association areas – forming the lexical and semantic bases of language.
D. Dyslexia

Dyslexia is a learning disability that occurs when a person does not properly recognize and process certain symbols, and the ability to read is impaired. Dyslexic people have difficulty understanding words, sentences, or paragraphs.

It may be visual, in which case the person has difficulty recognizing print (orthographic impairment). Visual processing is also slow.

It may be auditory, in which case the person has difficulty perceiving separate sounds in words (phonological impairment). They may also hear words with the phonemes scrambled. Tone deafness is another symptom.

It may be “attentional”, in which case letters migrate between neighboring words when reading (but are correctly identified and keep their correct relative position within the word), e.g. “fig tree” → “fig free”.

A neuroimaging (PET) study by Paulesu et al (2001) showed that the activated regions of cortex in the left hemisphere of dyslexic people during reading are “shrunken”, as compared to normal readers.
E. Parallel cognitive and lexical networks

The upward formation of higher cognitive categories (from specific & concrete to general & abstract) in association cortex is likely accompanied by the parallel formation of a lexical-semantic system in posterior cortex, representing the words corresponding to cognitive categories. Presumably, these parallel network systems (cognitive and lexical) may activate one another. Neuroimaging (PET) evidence indicates that the cortical areas activated by pictures of objects are also activated by the words symbolizing those objects.

A similar parallel lexical network system may form in frontal cortex for symbolic word representations of action. The lower levels of this system (Broca’s area & associated cortical areas) represent the function words necessary for syntax. The higher levels (premotor & prefrontal areas) represent verbs (action words) that “symbolize higher memory networks of action”.
Cortical dynamics of syntax

Which part of the brain imposes the rules of syntax in language?

The frontal cortex must provide the ordering function of syntax, just as it does for the ordering of all behaviors.

Syntax is a temporal ordering. The meaning of sentences comes from ordering words in particular sequences. (Note that the temporal order in language requires conversion from a spatial order in the brain since memory networks for words are distributed spatially in the cortex.)

Aphasic speech may be due to lesions of classical (Broca’s area) or non-classical (e.g., premotor or cingulate cortex) regions. Patients with prefrontal lesions also may have speech disorders, but they are more subtle than Broca’s aphasia. Speech is “superficial and structurally weak”. It has few dependent clauses or qualifications.

The impairment of syntactic processing seen with these lesions is part of a larger impairment that transcends language – it is an impairment of the organization of behavior. In other words, the disorder of the syntax of language is an expression of a general disorder of the syntax of action.