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 question 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 cognits, 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.

Animals such as the salamander have minimal conspecific communication. Communication is greater in animals with more developed brains such as primates.

There are corresponding differences in brain anatomy.

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.

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

Expansion and elaboration of the limbic regions provides the primate with the ability to communicate instinctively and emotionally with conspecifics. Expansion and elaboration of the lateral neocortex further provides humans with the substrate of language.
Language depends on both lateral neocortex and limbic structures.

The dependency 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

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 cognits 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).

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.
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.
Hemispheric lateralization

In most people, linguistic function is lateralized to the left hemisphere.

1. Review of the lateralized nature of sensory & motor systems

a. Somatosensory system: cortical lesion --> contralateral *hemianesthesia* -- impaired somesthesis

b. Visual system: cortical lesion --> contralateral *hemianopsia* -- defective visual field. Affects both eyes.

c. Motor system: cortical lesion --> contralateral *hemiparesis* (body weakness) or *hemiplegia* (paralysis)
2. Evidence of lateralization from the *Wada test*

**Wada test**: injection of sodium amytal (a barbiturate) into carotid artery selectively puts to sleep left or right hemisphere for several minutes and thus is used to differentiate left vs right hemispheric function. It shows that hemispheres have both language & emotional differences.

a. Principally used for determining the side of language dominance in pre-surgery epileptic patients.

Patient instructed to speak continuously while sodium amytal is injected. If hemisphere dominant for speech is affected, patient stops speaking & does not respond to a command to continue.
Language lateralization was studied by Rasmussen & Milner (1977):

96% of right handers have left representation
4% of right handers have right representation
70% of left handers have left representation
15% of left handers have right representation
15% of left handers have bilateral representation

Childhood left hemisphere lesions may cause shifts to right or bilateral representation in either right- or left-handers.

b. In addition to the effect on language, sodium amytal can affect mood.

left injection --> brief depression
right injection --> euphoria
3. Evidence of lateralization as determined by left hemisphere lesions

Usually patients don't have a single impairment, but show a complex pattern of symptoms. Most patients show the following symptoms due to left hemisphere lesion:

a. *dysarthria* -- impaired speech articulation  
b. *aphasias* -- disturbances of language comprehension  
c. *apraxias* -- impaired ability to carry out purposeful movement -- not paralysis or inability to comprehend instructions. (may affect both sides of body but typically occurs with left cortical lesions.)  
   e.g. use of objects (blow out match)  
   or symbolic gestures (stick out tongue)
d. Conclusion about left hemisphere function

It is primarily specialized for language in most people. It supports functions such as:

i. reading
ii. writing
iii. understanding & speaking
iv. verbal ideation
v. verbal memory
4. Evidence of lateralization as determined by right hemisphere lesions

a. impaired spatial orientation -- manifested by reduced ability to perform block constructions, copy drawings or interpret maps. Includes difficulty in extrapersonal space, e.g. noting differences in external landmarks; & intrapersonal space, e.g. distinguishing left from right.

b. dressing apraxia -- reduced ability to dress

c. neglect of left visual field -- cardinal feature of extrapersonal space disorder for right hemisphere disease; not blind, but rather unaware examples: word crowding (recovery may subsequently occur) crowding of numerals on clock

Neglect of right side of space rarely seen in patients with left hemisphere lesions

d. visual (discriminative) agnosia -- impaired recognition of visual forms, e.g. interpretation of flowers as arrows, face recognition
e. Conclusions about right hemisphere function

i. manipulospatial skills -- e.g. block arrangement
ii. representation of non-verbal form e.g. abstract drawing, patterns of dots, line figures
iii. face recognition
iv. recognition of musical stimuli
5. Split-brain experiments

a. Anatomy

**Corpus Callosum (C.C.)** -- bidirectional fiber pathway connecting left & right cortex
3 parts:
i) anterior genu -- between frontal lobes
ii) medial body -- between temporal & parietal lobes
iii) posterior splenium -- between occipital lobes

**Anterior Commissure (A.C.)** –pathway connecting medial temporal lobe structures, e.g. amygdala

As a general rule, fibers from a particular layer of cortex in 1 hemisphere project to & receive from the same region & layer of opposite hemisphere.
b. History

Before 1960's, the role of the C.C. was not known. As recently as 1950, Lashley facetiously expressed the opinion that C.C. only serves to keep the hemispheres from sagging.

Then neurosurgeons began to cut the C.C & A.C in cases of severe intractable grand mal epilepsy to prevent the spread of epileptic seizures from one hemisphere to the other.

In a series of studies in 1960's, Roger Sperry with Michael Gazzaniga tested split-brain patients.

Sperry had worked with animals with C.C. sections. He cut optic chiasm in addition to C.C. & A.C. Animal trained to make visual discriminations with 1 eye. When tested with untrained eye, they behaved as if completely naive. The training experience was limited to 1 hemisphere.
c. Hemispheric differences in split-brain patients

Human patients with *split brains* normally do well in real-life situations because both hemispheres normally obtain common info. E.g. as eyes scan environment, each hemisphere receives complete representation of surroundings.

Sperry & Gazzaniga set up expt so hemispheres received different info. Used brief tachistoscopic visual stimuli projected to rt or left vis. field. Transmitted only to opposite hemisphere (optic chiasm not cut)
Classical expt -- apple presented to right visual field & asked what was seen -- answered "apple".
When presented to left visual field, denied seeing anything. If prompted, would guess or make up answer. However, patient could identify the object by pointing to it or picking it out manually from several others -- using tactile cues. Suggests that learning, memory, motor coordination intact in right hemisphere.
The right hemisphere is almost totally incapable of language output, but can process simple linguistic input. It does have some primitive understanding of language. Many words projected to right hemisphere can be read & understood. Letters D-O-G projected in left visual field, patient could pick model of dog with left hand. More complicated commands not understood.
d. Hemispheric competition

Hemispheres sometimes are seen to interfere with each other.

When patients do block task with the left hand, controlled by the right hemisphere, the left hemisphere sometimes tries to interfere with task. It can impede successful completion by interference with right hand. The left hemisphere also sometimes initiates verbal comments about performance of the non-dominant hemisphere.
e. Chimeric face experiments

What happens when a split-brain patient is put in a situation where either hemisphere can take control? Levy, Trevarthen & Sperry (1972) showed chimeric faces to split-brain patients.

When shown picture with fixation pt in middle, verbal report is that of right side of face. As expected, left hemisphere responds verbally.
What happens when a non-verbal response is required?
Either hemisphere could potentially direct behavior. Presumably either side could respond when asked to point when shown a series of whole faces. However, patients pick the left-sided face.

Right hemisphere appears more competent at this & therefore it takes control.

Which 1 gains control seems to depend on which 1 is best suited for task to be performed.
f. Conclusions from split-brain experiments

Tasks that can be broken into logical elements in an analytic way are best performed by the left hemisphere.
*Left hemisphere is best suited to verbal encoding.

Tasks that require global processing of whole input are best performed by the right hemisphere.
*Right hemisphere is best suited to spatial-perceptual analysis.
6. Left-leaning asymmetries

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 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.

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, and memory are involved in language function.
7. Conclusions 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.
8. Evidence from bilingual subjects

After extensive left hemisphere damage, bilingual people usually lose both languages.

Some patients recover both languages in parallel.
Others recover one before the other.
Others recover the languages in steps with temporal alternation.

The native or most practiced language usually shows preferential recovery, but 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 topographies.
9. 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).

The conceptual centers may be seen to correspond to the frontal and posterior cortical association areas, substrates for high-level executive and perceptual cognits.
The acoustic center may be seen to correspond to the posterior language region, including Wernicke’s area, and also the *angular gyrus* (Brodmann area 39).

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

These lesions produce a deficit of recognition of structured language – called (semantic associative) agnosia.

Semantic associative agnosia is lack of recognition of words & sentences.

(Distinction between discriminative and associative agnosia derives from Lissauer, 1890, who distinguished “apperceptive” and “associative” agnosias.)

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

1. inability to name visually presented objects – implies impairment of cross-modal (visual-auditory) cognits
2. inability to understand written language – implies impairment of lexical cognits (vocabulary knowledge)
3. inability to identify object categories – implies impairment of categorical cognits (e.g., loss of ability to distinguish animate from inanimate objects, or fruits from vegetables)
**Conclusion**: the network hierarchies for perceptual memory also serve as the semantic substrate for language.

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

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

At the highest levels, other transmodal cognits are formed by categorical and conceptual associations. The word sounds associated with categories and concepts may be organized in parallel lexical networks.
**Conclusion**: the network hierarchies for action and executive memory also serve as the productive substrate for language.

The *frontal linguistic hierarchy*:

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

Above this level is premotor cortex (BA6), containing cognits 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.

At the highest level:
  a) medial prefrontal cortex, especially anterior cingulated 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: low speech fluidity & spontaneity; impoverished linguistic structure – lack of ability to conceptualize, plan, and execute complex linguistic structures.
Double dissociation of linguistic categories in frontal & posterior regions

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 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

Verbs elicit larger ERP components than nouns at frontal locations. Nouns elicit large 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

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 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 large, long-lasting (400 ms) 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 (Fig. 7.4), 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

In deaf, late English learners, English only activates areas in right hemisphere. In all signers, ASL also activates areas in right hemisphere.
Interpretation:
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 cognits 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 cognits.
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 cognits to first represent syllables, then words, and then syntax in surrounding non-classical areas.

3. With continuing experience, the cognits built around the core language areas become associated with cognits 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-executive 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 cognits of action”.
Cortical dynamics of syntax

How does the brain impose the rules of syntax on language?

In other words, how is syntax used by the brain to understand and produce the proper structure of phrases and sentences?

Fuster’s answer: the frontal cortex provides the ordering function of syntax.

Syntax is a temporal ordering. The meaning of sentences comes from ordering words in particular sequences.

Since cognits for words are distributed spatially in the cortex, implementation of syntax requires that a spatial order in the brain be converted into a temporal order in language.

From the deficit in making syntax in Broca’s aphasia, we know that syntax involves Broca’s area and surrounding cortex. Spoken language in Broca’s aphasia lacks the lexical elements, such as function words, that make syntax possible, even though the temporal order of that speech is still intact.
Aphasic speech due to premotor or cingulate lesions is more verbally productive, but syntax is still limited to short, simple, automatic speech that lacks spontaneity and prosody.

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 transcends language – it is an impairment of the organization of behavior. Therefore, the disorder of the syntax of language is an expression of a general disorder of the syntax of action.

The production of language requires a cognit for syntactic temporal structure (action schema) in frontal cortex to continuously interact with cognits of the lexical-semantic system in posterior cortex that provide meaningful content words. This interaction may be a form of the perception-action cycle.

In this interaction, both frontal and posterior networks provide the lexicon, whereas frontal networks also provide the grammar.

Working memory is used to provide temporal integration when the meaning of speech parts must be maintained over time to produce or comprehend language.