Language and the Brain

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Many species have evolved sophisticated communication systems, but human language stands out as special in at least two respects, both of which contribute to the vast expressive power of human language. First, humans are able to memorize many thousands of words, each of which encodes a piece of meaning using an arbitrary sound or gesture. By some estimates, during the preschool and primary school years a child learns an average of 5-10 new words per day, on the way to attaining a vocabulary of 20,000-50,000 words by adulthood. Second, humans are able to combine words to form sentences and discourses, making it possible to communicate infinitely many different messages, and providing the basis of human linguistic creativity. Furthermore, speakers are able to generate and understand novel messages quickly and effortlessly, on the scale of hundreds of milliseconds. Linguists and cognitive neuroscientists are interested in understanding what special properties of the human brain make such feats possible. Efforts to answer this question go back at least 150 years. A great deal of attention has been given to the issue of which regions of the human brain are most important for language, first using findings from brain-damaged patients, and in recent years adding a wealth of new information from modern non-invasive brain recording techniques such as *positron emission tomography* (PET) and *functional magnetic resonance imaging* (fMRI). However, it is important to bear in mind that knowing where language is supported in the human brain is just one step on the path to finding what are the special properties of those brain regions that make language possible.

Classic Aphasiology. 19th century studies of *aphasic* syndromes, which are selective impairments to language following brain damage, demonstrated the importance for language of a network of left-hemisphere brain areas. Although this work was extremely difficult, requiring neurologists to compare language profiles with autopsy findings sometimes years later, the main findings have been largely confirmed, at least in their broad outlines. It is estimated that around 95% of right-handers and 70% of left-handers show left-hemisphere dominance for language. In terms of more specific brain regions, the model proposed by the 26-year old German neurologist Carl Wernicke in 1874 has proven to be remarkably accurate for clinical purposes. Wernicke classified language areas primarily in terms of the *tasks* that they were responsible for. Damage to the left inferior frontal gyrus is associated with a syndrome in which language comprehension appears to be relatively intact but language production is severely impaired, showing halting speech and pronounced difficulty with function words such as determiners (e.g., *the, a, this*) and auxiliary verbs (e.g. *is, would, can*). The brain area is known as *Broca's Area* (also known as Brodmann's areas 44 and 45) and the syndrome as *Broca's aphasia*, following Paul Broca, who in 1861 was the first to claim a link between that brain area and language. Wernicke proposed that Broca's Area is specialized for the task of converting mental representations of language (which he assumed to be fundamentally auditory in nature) into speech. Damage to an area in the superior posterior part of the left temporal lobe (*Wernicke's Area*; Brodmann's area 22) was associated with a different syndrome (*Wernicke's aphasia*), in which language comprehension was seriously compromised and language production was grammatically fluent but often semantically inappropriate or lacking in coherence. Wernicke proposed that this second area was responsible for decoding and storing auditorily presented language. Wernicke's model and an updated account presented by Norman Geschwind in the 1960s made a number of additional predictions about specific kinds of neural damage that should lead to specific language impairments (e.g., speech and comprehension problems without impairment to repetition), and stands out as a landmark in efforts to understand mind-brain relations.

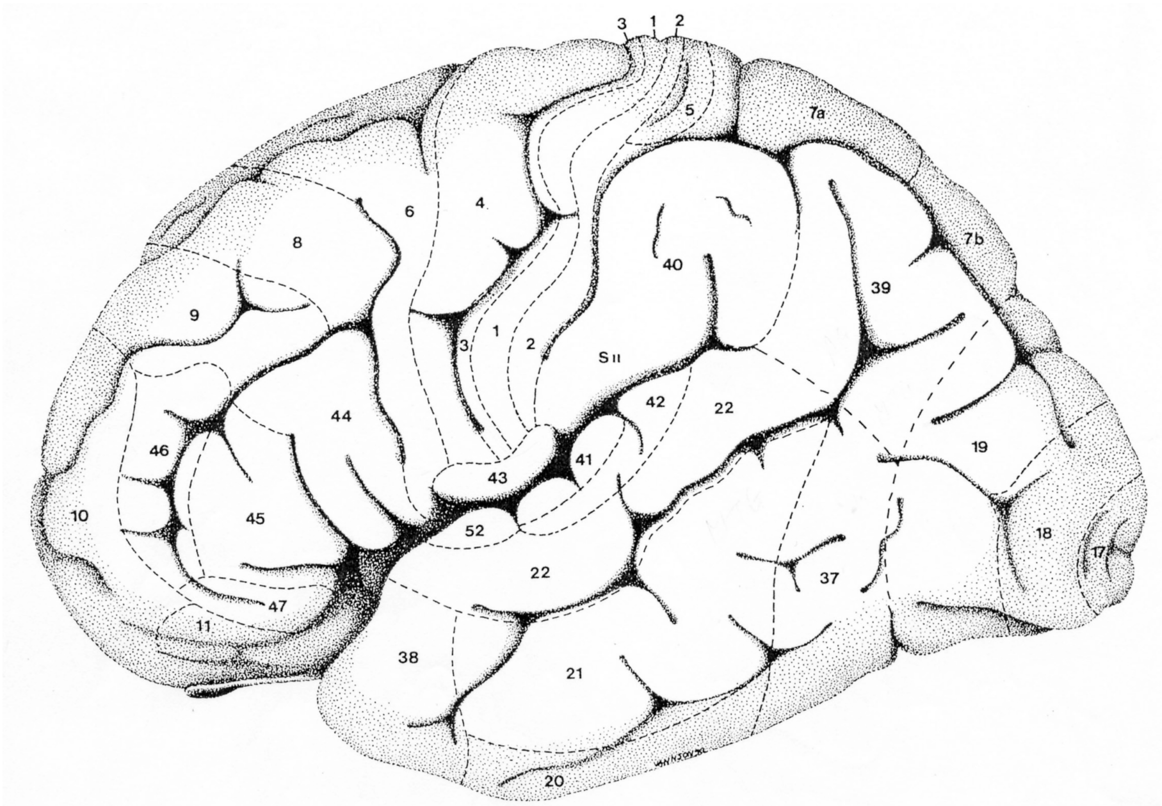

Figure 1: Cortical Language Areas (Broca's Area = BA45; Wernicke's Area = BA22)

Modern Aphasiology. Whereas the classic model of aphasia emphasized a division of language areas based on tasks (e.g., speaking, understanding), modern aphasia research suggests that it may be more appropriate to differentiate language areas based on the types of information that they preferentially deal with, such as syntax, phonology, or semantics. The most obvious clinical symptom of Broca's aphasia is labored language production, but careful studies from the 1970s onwards revealed that Broca's patients also have comprehension difficulties, particularly in situations where successful comprehension requires close attention to function words and inflectional morphemes. For example, individuals with Broca's aphasia often misunderstand who did what to whom in a passive sentence like *The dog was chased by the cat*. Findings such as these have led to the suggestion that Broca's Area has a task-independent role in syntactic processing that makes it important for speaking and understanding alike. Similarly, it has been suggested that Wernicke's area is responsible for semantic processes, both in speaking and understanding.

Functional Brain Imaging. The advent of modern non-invasive brain imaging technologies has had a major impact on the understanding of brain areas responsible for language. First, it is now straightforward to determine a patient's lesion site shortly after damage occurs, rather than waiting for autopsy. This has led to a dramatic increase in the database of knowledge available for deficit-lesion correlations. The crucial role of left-inferior frontal regions for language production and syntax has been strongly supported, although important correlational studies by Nina Dronkers suggest that the clinical symptoms of Broca's aphasia may be most strongly associated with a deeper left frontal structure called the *insula*. Second, techniques such as fMRI can be used to test for correlations between selective activation patterns in normal adults and selective deficits in patients. This work has largely confirmed the importance of classic left frontal and temporal language areas, but has highlighted a number of additional left-hemisphere language areas, predominantly in the frontal and temporal lobes. Third, brain stimulation studies using *Transcranial Magnetic Stimulation* (TMS) have made it possible to noninvasively apply stimulation to create momentary activation or impairment in highly specific cortical regions. Stimulation studies are important, because they can show that a particular area is essential for a specific task rather than merely involved in that task. To-date there have been very few TMS studies of language, but their findings largely support the conclusions of deficit-lesion correlation studies in patients. Fourth, it has become apparent that some classic language areas are also implicated in non-language tasks. For example, Broca's area has been implicated in studies of motor planning and short-term memory for verbal items. This raises the possibility that brain areas previously thought to be specialized for specific types of language task or linguistic information may in fact be specialized for specific types of mental computation, in a modality independent fashion. For example, both syntactic production and motor planning require the coordination and sequencing of a hierarchically organized plan.

Plasticity and Signed Languages. Although left-hemisphere dominance is the normal pattern, there is evidence for at least a limited degree of plasticity in the language system. In cases of children whose left hemisphere is removed early in life to control intractable epilepsy (e.g. before age 7-10 years) fairly good recovery of language abilities is typically observed. This indicates that the right hemisphere is able to take over many language functions if the left hemisphere is removed. Studies of signed languages indicate that the left-hemisphere remains very important for language even when it is conveyed through a different modality. Recent fMRI studies by Helen Neville and colleagues have shown that the processing of American Sign Language (ASL) recruited cortical areas in both hemispheres of native signers, while the processing of written English was left-lateralized. However, from the neuropsychological point of view, Ursula Bellugi and colleagues have shown that sign language aphasia is due primarily to left-hemisphere lesions.

Temporal Dynamics. In contrast to findings about the localization of language in the brain, studies using electroencephalography (EEG) and magnetoencephalography (MEG) measure the scalp voltages or magnetic fields generated by electrical activity in the brain, and provide a detailed record of the temporal dynamics of brain activity related to language. Studies of this kind have provided important clues about the mechanisms that allow language processing to be so fast and efficient. A family of different brain responses that appear within 100-600ms after the presentation of a linguistic event have been found to be highly sensitive to the predictability of the sound or word, suggesting that prediction of upcoming material plays an important role in rapid language processing.

Outlook. Advances in non-invasive brain recording techniques have led to dramatic improvements in the understanding of the localization and temporal dynamics of human language, but answers remain elusive regarding the underlying question of what special properties of the human brain allow it to support language. Non-human primates are able to learn small numbers of arbitrary pairings of symbol and meaning, and in the domain of words we need an explanation for why the human capacity for word learning is quantitatively greater than other primates. Meanwhile, non-human primates do not appear able to learn hierarchically organized grammatical systems, and thus in the domain of sentences we need an explanation for how human brains can rapidly encode systematic combinations of words, organized into recursive hierarchical structures. The current leading ideas on this question focus on the encoding of word combinations using the time-structure of neural activity, although it is unclear how this could capture the differences between humans and other primates, given the overall similarities across species in basic neural mechanisms. An important challenge for coming years will be to find whether the brain areas that are implicated in language studies turn out to have distinctive properties at the neuronal level that allow them to explain the special properties of human language.

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