

Neural organization and plasticity of language

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Powerful advances in neuroimaging techniques have added to and refined classical descriptions of the neurobiology of language in adults. Recent studies have employed these methodologies to study the nature and extent of plasticity of language-relevant aspects of cerebral organization in adults, in early and late bilinguals and in people who have acquired language through different modalities. Studies of children have documented dynamic shifts in cerebral organization over the course of language acquisition. Each of these different approaches has revealed constraints on the identity of the neural systems that mediate language; these studies have also described the marked and specific effects of language experience on the organization of these systems.

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Abbreviations

ASL	American Sign Language
ERP	event-related brain potential
fMRI	functional magnetic resonance imaging
MEG	magnetoencephalography
PET	positron emission tomography

Introduction

Improvements in the capabilities and accessibility of neuroimaging techniques have permitted increasingly differentiated characterizations of the neural systems central to cognition in the adult brain. A key issue that has been much less investigated concerns the degree to which these characteristic aspects of cerebral organization are invariant and strongly biologically determined and the role of environmental input in their final form. Extensive research within the domain of sensory processing has documented the existence of strong biases that constrain development and, in addition, has revealed considerable adaptation and reorganization following alterations of sensory input.

This review will discuss recent studies from the past two years directed toward these issues within the domain of human language, which we have grouped into three main sections: first, the neurobiology of language in adults; second, alterations in the organization of the language systems of the brain in adults who have had different and specific alterations of language experience; and third, the neurobiology of language acquisition during development.

Organization of language in normal adults

Studies of the neurobiology of language have long been dominated by the classical view, which emphasized the role of three well-circumscribed cerebral regions within the left hemisphere: Broca's area in the inferior frontal lobe, for planning and executing speech; Wernicke's area at the junction between the superior temporal and the parietal lobes, for the analysis and identification of speech; and the angular gyrus, described by Dejerine in 1892, for orthographic to phonological decoding during reading. This view emerged from studies of the effects of damage to different brain regions on specific language skills. Recently, the advent of noninvasive neuroimaging techniques, such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI), event-related brain potentials (ERPs) and magnetoencephalography (MEG), has permitted the investigation of language organization in healthy individuals and has also permitted more accurate identification of the extent of damage in individuals with aphasia [1-3,4**].

Studies employing these techniques have confirmed the importance of classical language-related areas within the left hemisphere; however, they have also suggested three other important aspects of the organization of language in normal adults. Firstly, these imaging studies have indicated that language centers are not well circumscribed, homogeneous areas, but, rather, consist of small, nonadjacent, focal spots specialized for specific components of language [5,6]. Second, language-related activation is observed not only in classical language-related brain areas but also outside these centers, such as most of the left perisylvian cortex, including the entire extent of the superior temporal gyrus and temporal pole, the lingual and fusiform gyri, middle prefrontal areas (dorsolateral prefrontal cortex) and the insula [6-9]. Third, the functional role of the language-related areas is more accurately characterized in terms of linguistically relevant systems, such as phonology, syntax and semantics, than in terms of activities, such as speaking, repeating, reading and listening [4**,10-13].

While the identity and precise role of the various language-related areas are still being determined, some general principles are emerging. Analysis of visual word form recruits early visual areas, including the left extrastriate visual cortex and inferior temporal areas [7,14]. Access from word forms to phonemic knowledge appears to be mediated by structures along the middle temporal gyrus. Interestingly, this intermediate stage of lexical retrieval seems to be divided into anatomically separable subsystems that are organized by different word categories, such as verbs and nouns, and, within nouns, tools, foods, or body parts [15,16**,17,18]. Within the auditory

modality, the differential processing of speech sounds from that of equally complex acoustic stimuli occurs early within the supratemporal auditory cortices [19,20*,21]. Further phonological processing occurs within posterior temporal areas somewhat inferior to the classically defined Wernicke's area [22,23*]. The many recent investigations of the role of Wernicke's area in phonological processing suggest that it is not a functionally homogeneous area [24]; rather, it contains distinct regions mediating processes as varied as auditory word processing and verb generation [22]. Multiple lines of evidence argue for a separate level of syntactic analysis during lexical and sentence processing [4**,11,12,25]. Studies of different and specific syntactic operations suggest that whereas overall syntactic processing appears to engage most of the left perisylvian cortex [25–27], separate subcomponents may have different, focal generators [11,13,28,29]. A common requirement of syntactic processing is the integration and maintenance of information over time as a sentence unfolds. This aspect of syntactic processing requires verbal short-term memory, a process that includes areas within inferior prefrontal areas and, in particular, Broca's area [26,27,30**,31].

Adult plasticity: reorganization of language systems following brain damage and training

As described above, both studies of the effects of brain damage and studies employing neuroimaging techniques consistently describe a greater role for the left hemisphere in speech and language in most adults. Control of the production of speech is ubiquitously lateralized and is a hallmark feature of hemispheric specialization in humans. Therefore, of considerable interest are two recent reports of the new development of speech production capabilities within the right hemisphere of an adult several years following callosotomy [32,33]. Within the domain of language comprehension, investigators have long noted recovery of function in adults with aphasia, but very little is known about its neural substrates. A recent ERP study has documented shifts in language lateralization that occurred with recovery from aphasia following strokes in adults [34**]. The patterns of recovery were different for different aphasia syndromes/lesion locations, raising specific hypotheses about the mechanisms of recovery of function. For example, typical Wernicke's aphasics display a shift of function to the right hemisphere that is long lasting, whereas patients with Broca's aphasia display a transient shift to the right hemisphere that is followed by a return to left laterality. These results suggest considerable long-term neural plasticity for at least some aspects of language. Consistent with this hypothesis are ERP studies of normal adults that have documented changes in language-related cerebral activity following specific language training [35,36**,37].

Developmental plasticity: effects of altered language experience during development

Sign language

An enduring issue in the neurobiology of language concerns the origins of the specialized role of language

areas within the left hemisphere and whether they arise from a specialization specifically for the processing of linguistic information or whether they are linked to more general aspects of processing, such as the sensory/motor information important in speech perception and production.

A powerful approach for examining this issue has been the comparison of the neurobiology of aural/oral spoken languages with that of visual/manual sign languages. Both signed and spoken languages are highly structured systems displaying constraints at many levels of linguistic analysis, and they display similar developmental timetables and critical periods. However, the surface forms of signed languages are markedly different than those of spoken languages: the former depend upon contrasts of visual spatial location and motion, whereas the latter depend upon the perception of rapidly changing auditory spectral information. Despite these differences, studies of the effects of brain damage on sign language report a central role for the left hemisphere, suggesting that its role in language derives from higher-order properties of language [38]. In addition, studies of sign aphasia have provided evidence for a role of the right hemisphere in aspects of sign comprehension [39].

Recent PET, fMRI and ERP studies of sign processing in neurologically intact individuals report many similarities in the patterns of activations within the left hemisphere for both signed and spoken/written language [40–42,43*]. In addition, however, in contrast to the pattern for spoken language, fMRI and ERP studies of both deaf and hearing native signers report large activations within the right hemisphere during sign comprehension [41,43*]. This inclusion of the right hemisphere in the language system may only occur during a limited, critical period of development, as similar activation is not observed in late learners of American Sign Language (A Newman *et al.*, *Soc Neurosci Abstr* 1997, 23:1059). These results, which demonstrate the activation of classical left hemisphere language areas during the processing of native languages of markedly different form and modality, emphasize strong biases of the left hemisphere in processing higher-order aspects of language. The activation of the right hemisphere in early learners of sign language reveals the additional role of specific processing requirements of the language in determining the final organization of language systems of the brain. A key goal for future research along these lines, as in all research in neuroplasticity, is to specify the effects of different ages of occurrence of the altered language experience.

Bilingualism: effects of early and late acquisition of a second language

Over the past several decades, studies of the effects of brain damage in bilinguals have reported cases in which one of the languages learned is lost while another is spared

[44,45]. Imaging studies of normal adults have begun to explore the hypothesis, raised by these observations, that the neural representation of different languages is different in bilingual individuals. Observers have long noted the greater facility with which young children, compared to adults, acquire a second language. This raises the related hypothesis that the representation of a second language will differ depending on age of acquisition of the language. Most studies to date have studied 'late' bilinguals.

PET, fMRI and ERP studies all indicate strong left hemisphere activation for the native language in bilinguals [46•,47–49]. Second languages learned late (i.e. after 7 years of age) are organized within neural systems that are partially or completely nonoverlapping with those for the native language. These systems for later-learned languages tend to be less lateralized and display a high degree of variability between individuals [46•,47–50]. By contrast, the few studies that have included early bilinguals report overlapping areas of activation for native and second languages [48,50]. Moreover, some results indicate there may be considerable specificity in the age of acquisition effects. For example, the age of acquisition of the second language appears to have more pronounced effects on the organization of frontal than posterior areas of the left hemisphere [50] and has stronger effects on grammatical processing and related brain systems than on semantic processing [48].

Two recent studies raise hypotheses about the role of different subcortical structures in first and second language acquisition. Aglioti *et al.* [45] report that a patient with a lesion to the left basal ganglia led to a long-lasting aphasia of the native language while sparing a later-learned language. Dehaene *et al.* [46•] report fMRI activation of the anterior cingulate during processing of a later-learned but not a native language. These results are consistent with the proposed roles of the basal ganglia in automatic, implicit processing and of the anterior cingulate in attentive, controlled tasks (see also [29]).

Future studies of different linguistic processes and of individuals who differ in age of language acquisition, degree of proficiency and degree of similarity between first and second languages will clarify the many factors important in the neural representation of different languages.

Development of neural systems for language

Recent papers continue the long-standing discussions concerning the degree to which the mechanisms that permit, and are employed in, language learning are specific to language or are domain general and employed in many other aspects of cognitive development [51–53]. Behavioral studies have refined characterizations of language acquisition and report data that are interpreted as support for the general nature of some aspects of language learning and the specificity of others [54–56].

Powerful evidence on the role of biological constraints and of experience in establishing cerebral systems for language have emerged from studies of cerebral specializations in infants and children of different ages and stages of language acquisition [2,57]. Investigators have long noted that brain lesions have markedly different effects on language in children than in adults. Recent studies employing refined methods of assessing different aspects of language and improved techniques for estimating the site(s) of damage confirm this general finding and raise specific hypotheses concerning the role of different brain regions in different aspects of language acquisition at different ages [58,59]. For example, early damage to left temporal regions is associated with deficits in grammar and in expressive language at all ages. However, perinatal damage to the right hemisphere is associated with deficits in vocabulary size only between 10 and 17 months of age, suggesting ongoing shifts in the roles of different brain regions in language acquisition across development.

Converging evidence for this proposal comes from ERP studies of normal children during primary language acquisition that document a central role for the right hemisphere during this same time period [60•]. Currently, the ERP technique is the optimal, noninvasive method for describing the role of different neural systems during primary language acquisition in normal infants, and it has just begun to be used in studies of these issues. Large, continual shifts in the configuration of language-relevant neural systems have been described in ERP studies of normal infants and children during the course of language acquisition [57,60•]. Some of these dynamic changes are linked to language capabilities and are independent of chronological age, whereas others appear to be determined more by age. Moreover, the time course of the changes and the degree of experience-dependent change displayed are different for different aspects of language [11,57].

Conclusions

Advances in behavioral methods of assessing different aspects of language and in neuroimaging techniques have begun to refine and add to descriptions of the neurobiology of language in adults, to characterize the effects of altered language experience on their organization and to describe their dynamic organization during primary language acquisition. Future studies will more precisely characterize the functional significance of different neural systems identified as important in language knowledge and will better separate and assess the roles of age of acquisition, language proficiency, structure and modality of language in determining cerebral organization for language. This approach will be complemented by the further characterization of the nature of the mechanisms that permit the rapid and ubiquitous acquisition of language during early childhood. Each of these lines of research will contribute to our basic understanding of the neurobiology of language and lays the foundation for studies of the neural bases of disorders of language.

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