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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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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Kutas M, King JW: **The potentials for basic sentence processing: differentiating integrative processes.** In *Attention and Performance 16: Information Integration in Perception and Communication. Attention and Performance*. Edited by Inui T, McClelland JL. Cambridge, Massachusetts: MIT Press; 1996: 501-546.

2. Thatcher RW, Lyon GR, Rumsey J, Krasnegor N (Eds): *Developmental Neuroimaging: Mapping the Development of Brain and Behavior.* San Diego, California: Academic Press; 1996.

3. Toga AW, Mazziotta JC (Eds): *Brain Mapping: The Methods.* San Diego, California: Academic Press, Inc.; 1996.

4. Osterhout L, McLaughlin J, Bersick M: **Event-related brain
•• potentials and human language.** *Trends Cogn Sci* 1997, 1:203-209.

This paper illustrates the use of ERPs to test the hypothesis that different linguistic processes elicit distinct patterns of neural activity, supporting the view that they are separable processes.

5. Schwartz TH, Ojemann GA, Haglund MM, Lettich E: **Cerebral lateralization of neuronal activity during naming, reading and line-matching.** *Brain Res* 1996, **4**:263-273.

6. Bavelier D, Corina D, Jezzard P, Padmanabhan S, Clark VP, Karni A, Prinster A, Braun A, Lalwani A, Rauschecker JP *et al.*: **Sentence reading: a functional MRI study at 4 Tesla.** *J Cogn Neurosci* 1997, **9**:664-686.

7. Nobre AC, Allison T, McCarthy G: **Word recognition in the human inferior temporal lobe.** *Nature* 1994, **372**:260-263.

8. Dronkers NF: **A new brain region for coordinating speech articulation.** *Nature* 1996, **384**:159-161.

9. Binder JR, Frost JA, Hammeke TA, Cox RW, Rao SM, Prieto T: **Human brain language areas identified by functional magnetic resonance imaging.** *J Neurosci* 1997, **17**:353-362.

10. Whitaker HA, Lecours AR (Eds): **Special Brain Issue.** *Brain Lang* 1995, **50.**

11. Friederici AD: **The temporal organization of language: developmental and neuropsychological aspects.** In *Communicating Meaning: The Evolution and Development of Language.* Edited by Velichkovsky B, Rumbaugh DM. Mahwah, New Jersey: Lawrence Erlbaum Associates; 1996:173-186.

12. Miozzo M, Caramazza A: **On knowing the auxiliary of a verb that cannot be named: evidence for the independence of grammatical and phonological aspects of lexical knowledge.** *J Cogn Neurosci* 1997, **9**:160-166.

13. Dronkers NF, Pinker S: **Language and the aphasias.** In *Principles in Neural Science.* Edited by Kandel E, Schwartz J, Jeffries T. Norwalk, Connecticut: Appleton and Lange; in press.

14. Price CJ, Wise RJS, Frackowiak RSJ: **Demonstrating the implicit processing of visually presented words and pseudowords.** *Cereb Cortex* 1996, **6**:62-70.

15. Spitzer M, Kwong KK, Kennedy W, Rosen BR: **Category-specific brain activation in fMRI during picture naming.** *Neuroreport* 1995, **6**:2109-2112.

16. Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR:
•• **A neural basis for lexical retrieval.** *Nature* 1996, **380**:499-505.

The authors present a lesion reconstruction study of patients with deficits in retrieving words in specific categories and a PET investigation of healthy subjects tested for word retrieval within distinct categories. Both studies indicate a reliable relationship between category-related word retrieval and neural sites in the left temporal lobe.

17. Martin A, Wiggs CL, Ungerleider LG, Haxby JV: **Neural correlates of category-specific knowledge.** *Nature* 1996, **379**:649-652.

18. Warburton E, Wise RJS, Price CJ, Weiller C, Hadar U, Ramsay S, Frackowiak RSJ: **Noun and verb retrieval by normal subjects: studies with PET.** *Brain* 1996, **119**:159-179.

19. Dehaene-Lambertz G: **Electrophysiological correlates of categorical phoneme perception in adults.** *Neuroreport* 1997, **8**:919-924.

20. Näätänen R, Lehtokoski A, Lennes M, Cheour M, Huotilainen M,
• Livonen A, Vainio M, Alku P, Llmoniemi RJ, Luuk A *et al.*: **Language-specific phoneme representations revealed by electric and magnetic brain responses.** *Nature* 1997, **385**:432-434.

The authors found an enhanced response (as measured by mismatch negativity using MEG) within the auditory cortex to phonemes of the participants' language as compared to phonemes of a language with which the participant is not familiar. This result suggests that speech-specific processing occurs as early as the auditory cortex.

21. Poeppel D, Phillips C, Yellin E, Rowley HA, Roberts TPL, Marantz A: **Processing of vowels in supratemporal auditory cortex.** *Neurosci Lett* 1997, **221**:145-148.

22. Fiez JA, Raichle ME, Balota DA, Tallal P, Petersen SE: **PET activation of posterior temporal regions during auditory word presentation and verb generation.** *Cereb Cortex* 1996, **6**:1-10.

23. Price CJ, Wise RJ, Warburton EA, Moore CJ, Howard D,
• Patterson K, Frackowiak RS, Friston KJ: **Hearing and saying. The functional neuro-anatomy of auditory word processing.** *Brain* 1996, **119**:919-931.

This study presents a PET investigation of the neural substrate involved in hearing and repeating single words – two landmark tasks in the aphasiology literature. This study establishes the contribution of different subregions within Broca's area to repetition and comprehension. It also illustrates the sensitivity of brain activation to the exact stimulus condition as well as the baseline considered.

24. Poeppel D: **A critical review of PET studies of phonological processing.** *Brain Lang* 1996, **55**:317-351.

25. Caplan D, Hildebrandt N, Makris N: **Location of lesions in stroke patients with deficits in syntactic processing in sentence comprehension.** *Brain* 1996, **119**:933-949.

26. Just MA, Carpenter PA, Keller TA, Eddy WF, Thulborn KR: **Brain activation modulated by sentence comprehension.** *Science* 1996, **274**:114-116.

27. Stromswold K, Caplan D, Alpert N, Rauch S: **Localization of syntactic comprehension by positron emission tomography.** *Brain Lang* 1996, **52**:452-473.

28. Jaeger JJ, Lockwood AH, Kemmerer DL, Van Valin RD Jr, Murphy BW, Khalak HG: **A positron emission tomographic study of regular and irregular verb morphology in English.** *Language* 1996, **72**:451-497.

29. Ullman M, Corkin S, Coppola M, Hickok G, Growdon JH, Koroshetz WJ, Pinker S: **A neural dissociation within language: lexicon a part of declarative memory, grammar processed by procedural system.** *J Cogn Neurosci* 1997, **9**:266-276.

30. Fiez JA, Raife EA, Balota DA, Schwarz JP, Raichle ME,
•• Petersen SE: **A positron emission tomography study of the short-term maintenance of verbal information.** *J Neurosci* 1996, **16**:808-822.

This paper presents a PET investigation of the subcomponents of verbal short-term memory. Maintenance of verbal materials and covert articulation are compared. This study provides a detailed account of increases and decreases in blood flow associated with each condition.

31. Smith EE, Jonides J: **Working memory: a view from neuroimaging.** *Cogn Psychol* 1997, **33**:5-42.

32. Baynes K, Wessinger CM, Fendrich R, Gazzaniga MS: **The emergence of the capacity to name left visual field stimuli in a callosotomy patient: implications for functional plasticity.** *Neuropsychologia* 1995, **33**:1225-1242.

33. Gazzaniga MS, Eliassen JC, Nisenson L, Wessinger CM, Fendrich R, Baynes K: **Collaboration between the hemispheres of a callosotomy patient: emerging right hemisphere speech and the left hemisphere interpreter.** *Brain* 1996, **119**:1255-1262.

34. Thomas C, Altenmüller E, Marchmann G, Kahrs J, Dichgans J:
•• **Language processing in aphasia: changes in lateralization patterns during recovery reflect cerebral plasticity in adults.** *Electroencephalogr Clin Neurophysiol* 1997, **102**:86-97.

This study recorded ERPs and potential shifts during word processing to compare lateralization of language immediately after a stroke that led to aphasia and again several months later, after clinical recovery. Patients with different aphasia syndromes/lesion locations displayed different patterns of recovery, raising specific hypotheses about different mechanisms of recovery.

35. Kraus N, McGee T, Carrell TD, King C, Tremblay K, Nicol T: **Central auditory system plasticity associated with speech discrimination training.** *J Cogn Neurosci* 1995, **7**:25-32.

36. Abdullaev YG, Posner MI: **Time course activating brain areas in
•• generating verbal associations.** *Psychological Sci* 1997, **8**:56-59.
This ERP study documents striking changes in cerebral activation with practice in generating use for a visually presented noun. Left frontal and parietal activations were evident at the beginning of the task, but diminished rapidly with practice. When the subjects were required to generate a novel use for practiced words, the original activations within their left hemispheres reappeared together with new activations within right parietal areas.

37. McCandliss BD, Posner MI, Givon T: **Brain plasticity in learning visual words.** *Cogn Psychol* 1997, **33**:88-110.

38. Hickok G, Bellugi U, Klima ES: **The neurobiology of sign language and its implications for the neural basis of language.** *Nature* 1996, **381**:699-702.

39. Corina D: **Aphasia in users of sign language.** In *Language in Atypical Population.* Edited by Coppens P. Mahwah, New Jersey: Lawrence Erlbaum; 1997.

40. McGuire PK, Robertson D, Thacker A, David AS, Kitson N, Frackowiak RSJ, Frith CD: **Neural correlates of thinking in sign language.** *Neuroreport* 1997, **8**:695-697.

41. Neville HJ, Coffey SA, Lawson DS, Fischer A, Emmorey K, Bellugi U: **Neural systems mediating American sign language: effects of sensory experience and age of acquisition.** *Brain Lang* 1997, **57**:285-308.

42. Söderfeldt B, Ingvar M, Ronnberg J, Eriksson L, Serrander B, Stone-Elander S: **Signed and spoken language perception studied by positron emission tomography.** *Neurology* 1997, **49**:82-87.

43. Neville HJ, Bavelier D, Corina D, Rauschecker J, Karni A,
• Lalwani A, Braun A, Clark V, Jezzard P, Turner R: **Cerebral organization for language in deaf and hearing subjects: biological constraints and effects of experience.** *Proc Natl Acad Sci USA* 1998, **95**:922-929.
Cerebral organization during sentence processing in English and in American Sign Language (ASL) was characterized by employing fMRI at 4 Tesla. All groups, hearing and deaf, processing their native language, English or ASL, displayed activation within language areas of the left hemisphere. In addition, native signers, hearing and deaf, displayed extensive activation of homologous areas within the right hemisphere when viewing ASL.

44. Paradis M: **The cognitive neuropsychology of bilingualism.** In *Tutorials in Bilingualism: Psycholinguistic Perspectives.* Edited by de Groot AMB, Kroll JF. Mahwah, New Jersey: Lawrence Erlbaum Associates, Inc.; 1997:331-354.

45. Aglioti S, Beltramello A, Girardi F, Fabbro F: **Neurolinguistic and follow-up study of an unusual pattern of recovery from bilingual subcortical aphasia.** *Brain* 1996, **119**:1551-1564.

46. Dehaene S, Dupoux E, Mehler J, Cohen L, Perani D, van de
•• Moortele P-F, Lehèrici S, Le Bihan D: **Anatomical variability in the cortical representation of first and second languages.** *Neuroreport* 1997, **17**:3809-3815.
Bilingual subjects who acquired French (L1) as a native language and English (L2) after the age of 7 years listened to stories in L1 and L2 while fMRI images were obtained at 3 Tesla. While listening to L1, all subjects displayed asymmetrical activation of the left temporal lobe. By contrast, when listening to L2, these late learners displayed reduced lateralization of left temporal activity and considerable interindividual variability in the pattern of activation.

47. Perani D, Dehaene S, Grassi F, Cohen L, Cappa SF, Dupoux E, Fazio F, Mehler J: **Brain processing of native and foreign languages.** *Neuroreport* 1996, **7**:2439-2444.

48. Weber-Fox C, Neville HJ: **Maturational constraints on functional specializations for language processing: ERP and behavioral evidence in bilingual speakers.** *J Cogn Neurosci* 1996, **8**:231-256.

49. Yetkin O, Zerrin YF, Haughton VM, Cox RW: **Use of functional MR to map language in multilingual volunteers.** *Am J Neuroradiol* 1996, **17**:473-477.

50. Kim KHS, Relkin NR, Lee K-M, Hirsch J: **Distinct cortical areas associated with native and second languages.** *Nature* 1997, **388**:171-174.

51. Elman JL, Bates EA, Johnson MH, Karmiloff-Smith A, Parisi D, Plunkett K: *Rethinking Innateness: a Connectionist Perspective on Development.* Cambridge, Massachusetts: MIT Press; 1997.

52. Prince A, Smolensky P: **Optimality: from neural networks to universal grammar.** *Science* 1997, **275**:1604-1610.

53. Seidenberg MS: **Language acquisition and use: learning and applying probabilistic constraints.** *Science* 1997, **275**:1599-1603.

54. Saffran JR, Aslin RN, Newport EL: **Statistical learning by 8-month-old infants.** *Science* 1996, **274**:1926-1928.

55. Jusczyk PW, Hohne EA: **Infants' memory for spoken words.** *Science* 1997, **277**:1984-1985.

56. Markson L, Bloom P: **Evidence against a dedicated system for word learning in children.** *Nature* 1997, **385**:813-815.

57. Neville HJ, Mills D: **Epigenesis of language.** *Ment Retard Dev Dis Res Rev* 1997, **3**:282-292.

58. Bates E, Thal D, Trauner D, Fenson J, Aram D, Eisele J, Nass R: **From first words to grammar in children with focal brain injury.** *Dev Neuropsychol* 1997, **13**:275-343.

59. Nass R: **Language development in children with congenital strokes.** *Semin Pediatric Neurology* 1997, **4**:109-116.

60. Mills DL, Coffey-Corina SA, Neville HJ: **Language comprehension
• and cerebral specialization from 13 to 20 months.** *Dev Neuropsychol* 1997, **13**:397-445.
ERPs were recorded as children listened to words whose meanings they did or did not know. At 13 months of age, the differences between ERPs to known and unknown words were apparent over broad areas of both hemispheres, whereas at 20 months of age, these effects were only consistent over temporal and parietal regions of the left hemisphere. The results from studies examining children with different vocabulary sizes suggest a role for maturational factors and language skills in the specialization of language-relevant neural systems.