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EPIGENESIS OF LANGUAGE

Helen J. Neville[1]* and Debra L. Mills[2]

[1]Brain Development Laboratory, University of Oregon, Eugene, Oregon

[2]Center for Research in Language, University of California at San Diego, La Jolla, California

Studies employing event-related brain potentials (ERPs) and functional magnetic resonance imaging (fMRI) were designed to study the effects of different types of language experience on the development and organization of neural systems important in language processing. Comparisons of cerebral organization in normally hearing, monolingual English speakers with that observed in hearing and deaf late learners of English suggest that while systems important in lexical/semantic processing are relatively invulnerable to delays in exposure to a language, the development of systems important in grammatical processing, including the specialization of the left hemisphere, is affected by early language experience. Studies of individuals who acquired American Sign Language (ASL) as a native language suggest that similar systems within the left hemisphere are employed in processing all natural languages independently of the structure and modality of the language acquired. These studies also reveal that additional areas within the right hemisphere can be recruited into the language system when the language depends on the perception of spatial location and motion. Studies of children acquiring their first language reveal that there is increasing differentiation of the neural systems important in processing the meaning of words and of the areas important in lexical and grammatical processing and that these increases in specialization are linked to language abilities rather than to chronological age per se. Further studies suggest that developmental language impairment can result from alterations in one of several different systems important in language, and that some indices of these functional neural systems may be predictive of language impairment.

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Parsing a visual scene requires the participation and integration of numerous processes, including the perception of form, texture, spatial layout, color, motion, orientation, and depth. Extensive research at many levels of analysis from psychological to synaptic has shown that these different processes rely on different neural systems that develop at different rates and that these systems, while strongly biased to develop in a particular fashion, differ markedly in the degree to which and the time periods during which their development is dependent on and modifiable by input from the environment [Harwerth et al., 1986; Garraghty, 1993; Maurer, 1993; Neville, 1995; Neville and Bavelier, in press]. Little is known about the mechanisms that give rise to these striking differences in developmental specificity and plasticity, but ongoing research suggests they may be due to several factors, including differences in rates of maturation and in degree of redundant connectivity early in development.

Along similar lines, the comprehension and production of spoken language requires the participation and integration of numerous different processes, including the perception of rapidly changing acoustic spectra, of phonemes, the perception of a speaker's intentions and of context, social understanding, processes of shared attention, the processing of grammatical, lexical, and prosodic information, and motor planning, to name a few. It is reasonable to hypothesize, both on the basis of parsimony (in keeping with the evidence from visual development) and the available evidence, that each of these processes important in language use is mediated by different neural systems that develop at different rates and that these systems differ in the degree to which and the time period during which they are dependent on and are modified by language input.

In the research summarized here we have employed two techniques to characterize the location and timecourse of operation of the neural systems active during language processing in populations who differ in language experience. The event-related potential (ERP) technique permits high (millisecond) temporal resolution monitoring of the electrical potentials generated when people are presented with specific stimuli or cognitive demands. ERPs are recorded from metal electrodes placed on the scalp. Since ERPs are volume-conducted to the scalp, the spatial resolution is variable but can be around a centimeter. Functional magnetic resonance imaging (fMRI) permits the monitoring of changes in blood oxygenation associated with neuronal activity. The timecourse of hemodynamics limits the temporal resolution of fMRI (seconds); however, the spatial resolution is thought to be around a millimeter.

Neurobiology of Language in Monolingual and Bilingual Adults

Currently, rather little is known of the neurobiology of many of the processes important in language. In our work, we studied the development of the neural systems important in lexical semantic and grammatical processing. In normal, right-handed, monolingual adults, nouns and verbs (''open class'' words) that provide semantic information elicit a markedly different pattern of brain activity (as measured by ERPs) than do function words, including prepositions and conjunctions (''closed class'' words) that provide grammatical information in English

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*Correspondence to: Helen J. Neville, Brain Development Lab, 1227 University of Oregon, Eugene, Oregon 97403-1227. E-mail: neville@oregon.uoregon.edu

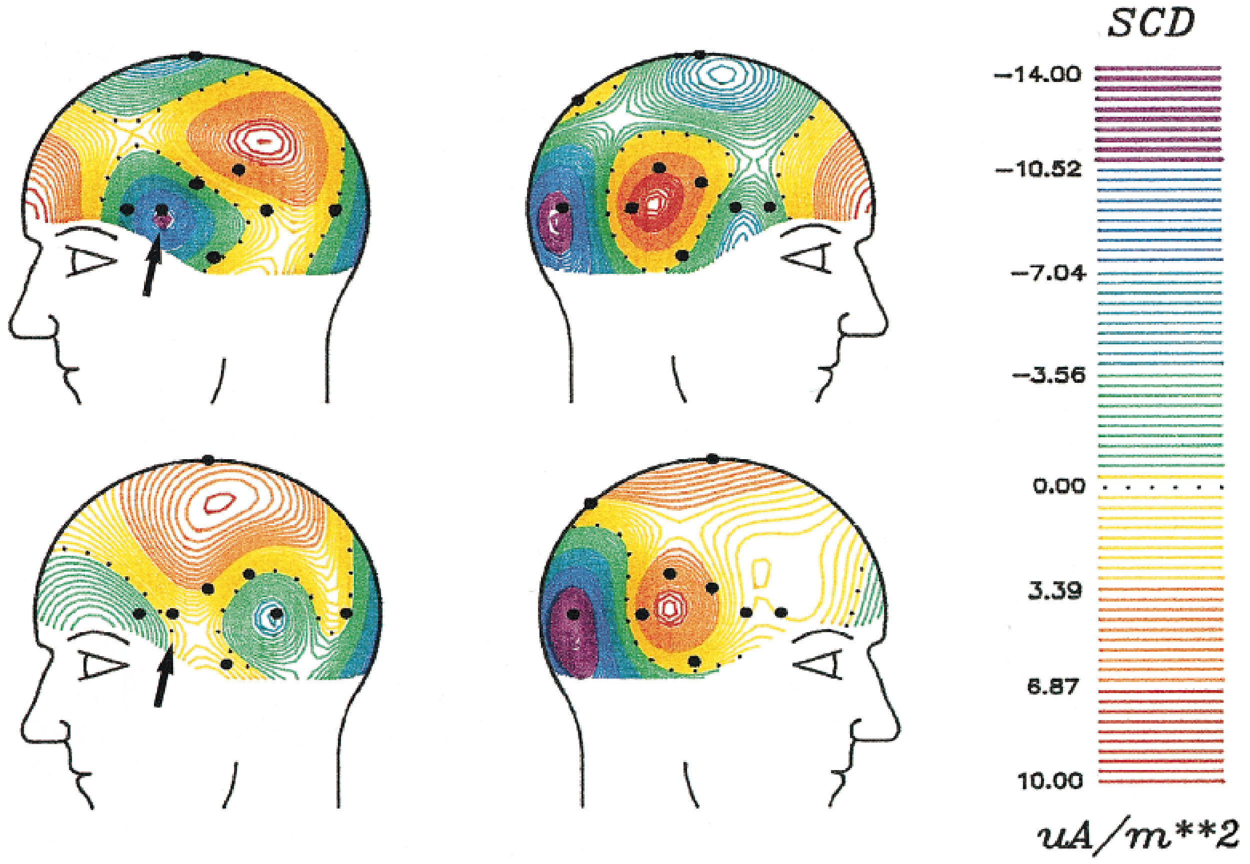

Fig. 1. Scalp topography of current source densities calculated for the N280 in response to closed-class words. Maps are averages across 17 hearing subjects (top row) and from 10 congenitally deaf subjects (bottom row). The longer wavelengths represent current sources (current flowing out of the head); the shorter wavelengths represent current sinks. Each map utilizes the same scale. The maps of the hearing and deaf subjects were similar over the right hemisphere. Over the left hemisphere the maps of hearing subjects display a prominent sink over the anterior temporal region that is absent in the maps from the deaf subjects (arrows). [Reprinted from Neville et al., 1992 with permission of Oxford University Press.]

[Neville et al., 1992]. In addition, sentences that are semantically nonsensical (but grammatically intact) elicit a different pattern of ERPs than do sentences containing a violation of syntactic structure (but that leave the meaning intact) [Neville et al., 1991]. These results are consistent with several other types of evidence that suggest different neural systems mediate the processing of lexical/semantic and grammatical information in adults. Specifically, they imply a greater role for more posterior temporal-parietal systems in semantic processing and for anterior temporal systems within the left hemisphere in grammatical processing (Fig. 1, top). This overall pattern appears ubiquitous in adults and many investigators have suggested that the central role of the left hemisphere in language processing is strongly genetically determined. Certainly the fact that most individuals, regardless of the language they learn, display left hemisphere dominance for that language indicates that this aspect of neural development is strongly biased.

Several lines of evidence demonstrate that even very strongly biologically determined aspects of development (including gene expression) depend on relevant aspects of the environment (ranging from the cell nucleus to the environment external to the animal) for their regulation, differentiation, and final form. To what extent are language-relevant aspects of cerebral organization dependent on and modified by language experience? One way we have investigated this question is to compare cerebral organization in individuals who learned English at different times in development. We have observed that in Chinese-English bilinguals delays of as long as 16 years in exposure to English had very little effect on the organization of the brain systems important in lexical semantics. In contrast, delays of only four years have significant effects on those aspects of brain organization linked to grammatical processing [Weber-Fox and Neville, 1996; Neville and Weber-Fox, 1994]. These results and parallel behavioral results (Fig 2) suggest that aspects of semantic and grammatical processing differ markedly in the degree to which they depend on language input. Specifically, grammatical processing appears very vulnerable to delays in language experience.

Studies of Deaf Adults

Further evidence on this point is provided by studies of congenitally deaf individuals who learn English late and as a second language (American Sign Language or ASL was the first language of our subjects). Remarkably, deaf subjects displayed ERP responses to nouns and to semantically anomalous sentences that were indistinguishable from those of normal hearing subjects who learned English as a first language. These data are consistent with the hypothesis that some aspects of semantic processing are largely unaffected by the many different aspects of language experience that differ between normally hearing and congenitally deaf individuals. By contrast, deaf subjects

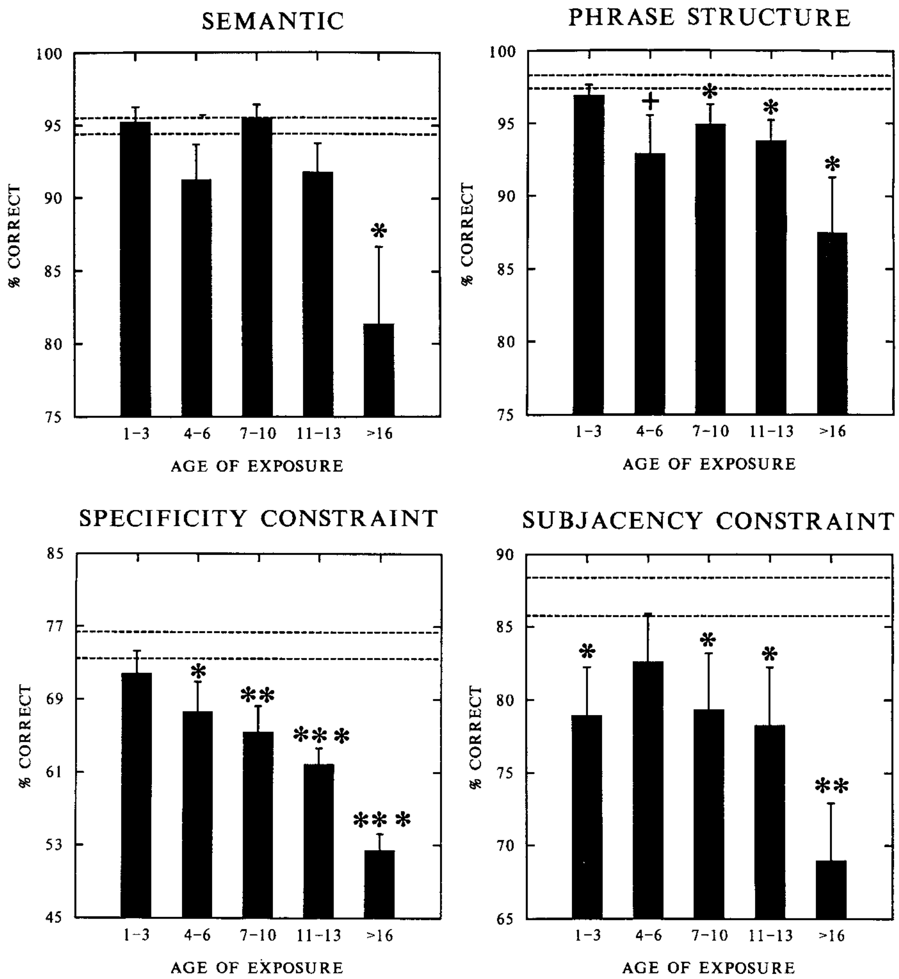

Fig. 2. Performance accuracy on judgments of experimental sentences: Semantic, Phrase Structure, Specificity Constraint, and Subjacency Constraint. Scores are grouped according to age of exposure to English: 1–3, 4–6, 7–10, 11–13, and >16 years. Double-dashed lines on each graph indicate the performance of previously tested monolinguals (mean ± the standard error). Scores that differed from monolinguals' performance are indicated (***P < 0.001, **P < 0.01, *P < 0.05, +P < 0.10). [Reprinted from Weber-Fox and Neville, 1996 with permission of the publisher.]

display aberrant ERP responses to grammatical information such as that presented in function words (Fig. 1, bottom). Specifically they do not display the specialization of the anterior regions of the left hemisphere that is characteristic of native, hearing learners. These data suggest that the systems that mediate the processing of grammatical information are much more modifiable and vulnerable in response to altered language experience.

Recently, we employed the fMRI technique to further pursue this hypothesis and also to obtain evidence on the question of whether the strongly biased role of the left hemisphere in language occurs independently of the structure and modality of the language first acquired [Neville et al., in press; Neville and Bavelier, in press; Bavelier, et al., in press]. As seen in Figure 3 (top), when hearing adults read English (their first language), there is robust activation within the left (but not the right) hemisphere and in particular within the inferior frontal (''Broca's'') regions. When deaf people read English (their second language, learned late and imperfectly) we did not observe activation of these regions within the left hemisphere (Fig. 3, middle). Is the lack of left-hemisphere activation in the deaf linked to lack of auditory experience with language or to incomplete acquisition of the grammar of the language? ASL is not sound-based but displays each of the characteristics of all formal languages, including a complex grammar that makes extensive use of spatial location and hand motion [Klima and Bellugi, 1979]. Studies of the same deaf subjects when viewing sentences in their native ASL clearly show activation within the same inferior frontal regions of the left hemisphere that are active when native speakers of English process English. These data suggest there is a strong biological bias for these neural systems to mediate language regardless of the structure and modality of the language acquired. However, if the language is not acquired within the appropriate time window this strong bias is not expressed. Biological constraints and language experience interact epigenetically, as has been described for many other systems in developmental biology.

The fMRI data also indicate a robust role for the right hemisphere in processing ASL. ERP studies of sentence processing in ASL confirm this general pattern of result [Neville et al., 1997]. These results suggest that language experience, in this case, the co-occurrence of location and motion information with language, shape the organization of the language systems of the brain. Furthermore, studies of late learners of ASL suggest there may be a critical period when the right hemisphere can be recruited into the language system [Neville et al., in press]. Much further research

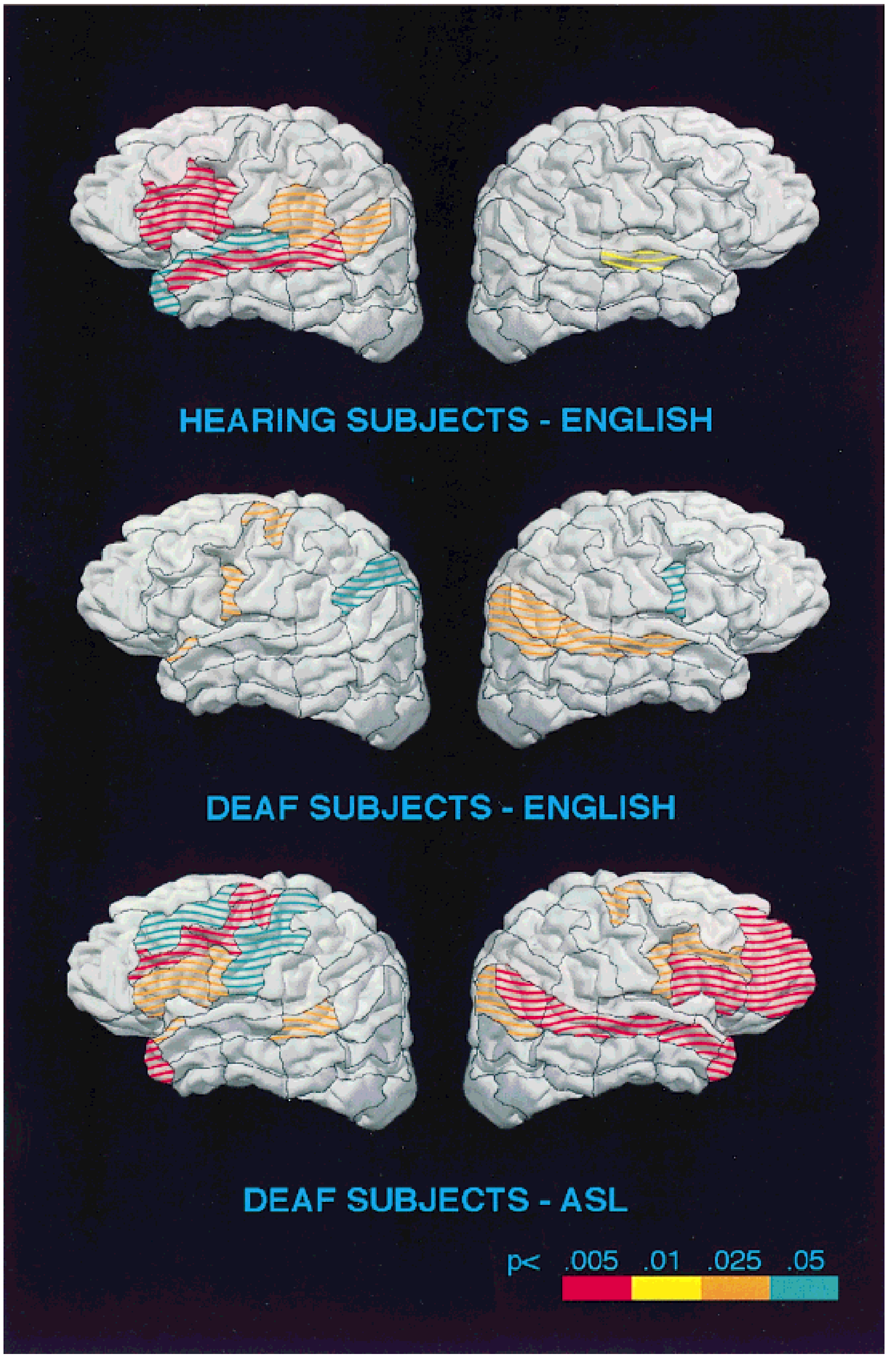

Fig. 3. Cortical areas showing increases in blood oxygenation on fMRI when normal hearing adults read English sentences (top), when congenitally deaf native signers read English sentences (middle) and when congenitally deaf native signers view sentences in their native sign language (American Sign Language).

is necessary to specify the different times in human development when different systems important in language depend on specific types of input for optimal development.

The Development of Cerebral Specializations in Infants and Children

The observation of different effects of language experience on lexical and grammatical processing suggests that these systems may develop at different rates during childhood. In ERP studies of sentence processing in children from 4 to 20 years of age, we have observed that semantically anomalous sentences elicit a very similar pattern of response in adults and children. However, the mature response to grammatical information presented in function words develops over a very protracted timecourse and emerges in the early to middle teen years. [Holcomb et al., 1992; Neville et al., 1994]. Thus these data suggest that the differences in developmental plasticity displayed by these different subsystems within language may be due in part to their different developmental timecourses. We have also been studying the differentiation of these language systems during the course of primary language acquisition in the first few years of life.

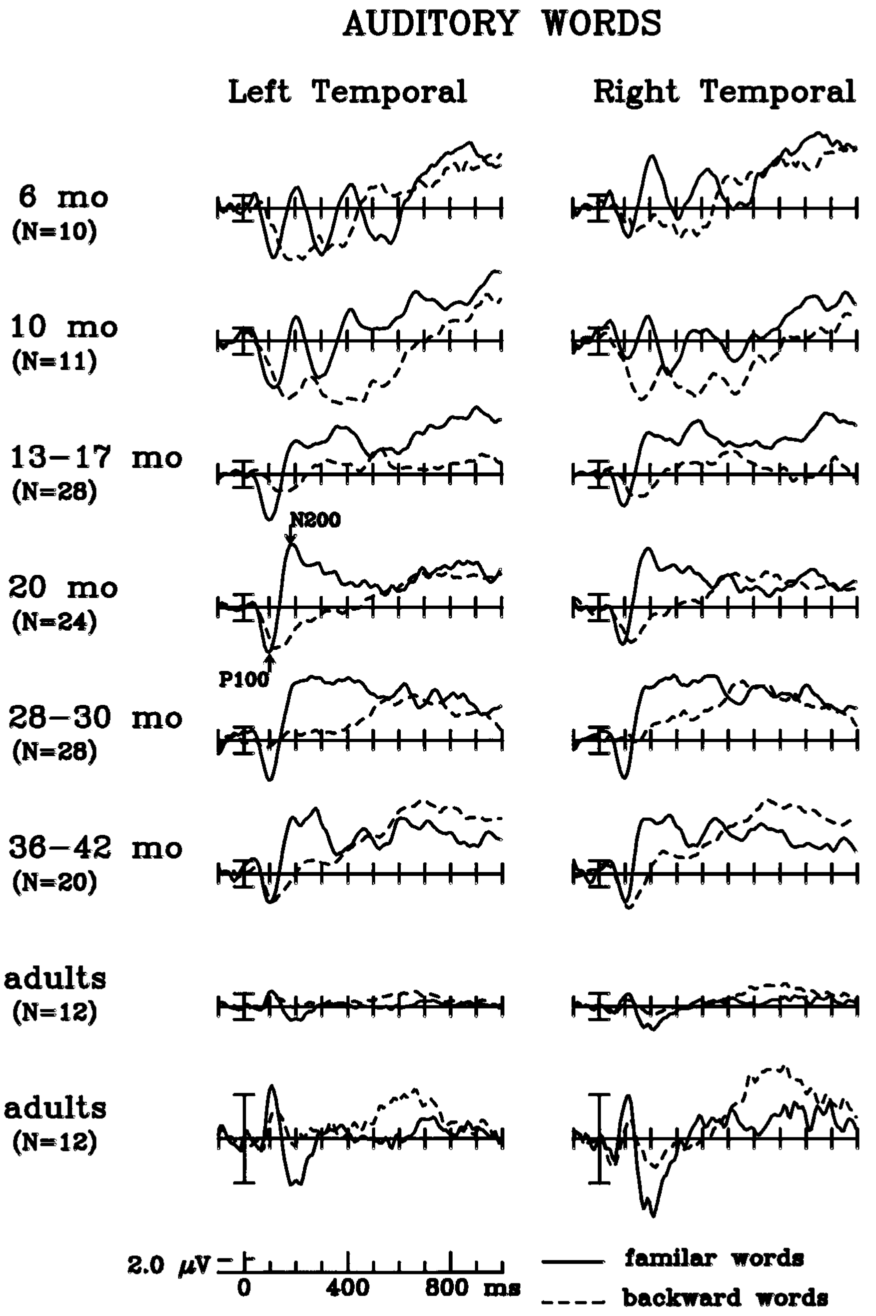

Fig. 4. ERPs to familiar words and backward words from infants 6–42 months and adults (adult ERPs displayed at two gains for comparison purposes). Words elicit a series of negative components that are absent or attenuated to backward words in all infant age groups. The morphology of ERPs to auditory words is markedly different for adults.

In normal adults, different parts of the brain are highly specialized for processing different types of information. Research with infants with focal brain lesions suggests that cerebral specializations within the language domain are different in infants and adults [Lenneberg 1967; Woods and Teuber, 1978; Basser, 1962; Aram and Eisele, 1992; Thal et al., 1991; Bates et al., 1997]. For example, although aphasia is almost exclusively associated with left-hemisphere damage in adults, there are relatively few differences in language outcome between children who sustained early left vs. right hemisphere brain injury. These findings raise the hypothesis that the neural systems that mediate different aspects of language in adults may not be the same systems that are important for early language acquisition.

We employed the ERP technique to study changes in cerebral organization to different types of language stimuli in infants as they pass through different ages and attain new language milestones. We tested children who were at the same chronological age but who varied in language abilities to separate changes that occur with chronological age from those linked to level of language abilities.

In this set of studies, ERPs were recorded as infants 6–42 months of age listened to a series of words [Mills et al., 1993, 1997]. The stimuli included familiar words, unfamiliar words, and backward words. For infants 13 months and older, the familiar words were words whose meanings were understood by the child. The unknown words were low-frequency English words that the child did not understand. The backward words were used to compare ERPs to words and provided a complex auditory stimulus with some of the physical characteristics of words. All three types of

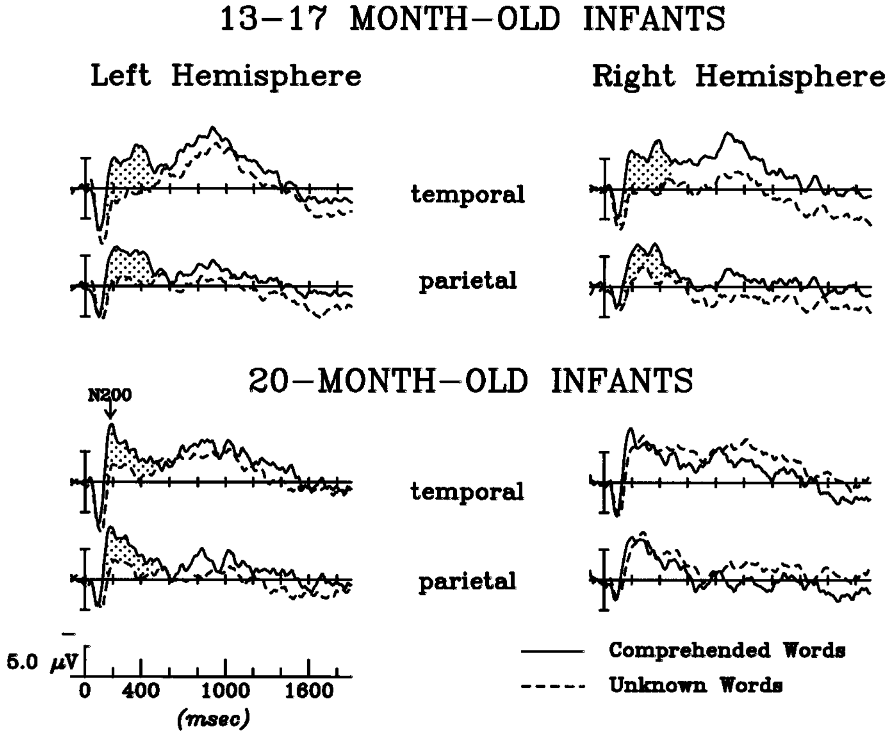

Fig. 5. ERPs elicited by comprehended and unknown words in 13–17 and 20-month-old children. At 13–17 months, ERPs to comprehended words are larger than to unknown words over several areas within both the left and right hemispheres. By 20 months, ERP differences to comprehended and unknown words are limited to temporal and parietal regions of the left hemisphere.

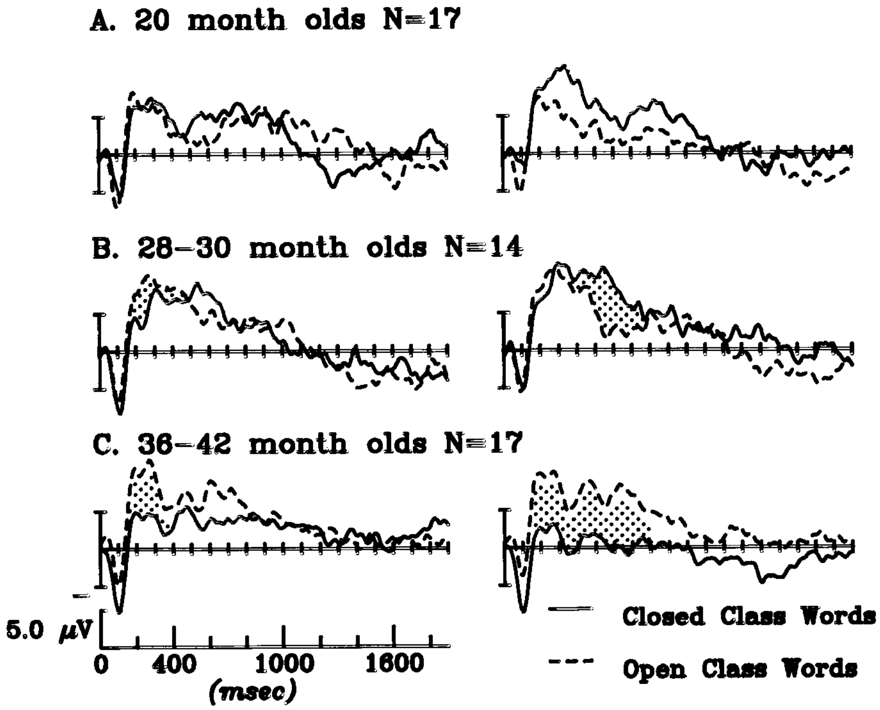

Fig. 6. ERPs to open- and closed-class words at three age groups: (**A**) At 20 months ERPs are not reliably different for open- and closed-class words (**B**) At 28–30 months ERPs to open- and closed-class words differ by 200 msec. ERPs to closed-class words are larger over the right than the left hemisphere. ERPs to open-class words are symmetrical. (**C**) At 36–42 months ERPs to open- and closed-class words show marked differences. ERPs to closed-class words show the more mature left greater than right asymmetry. ERPs to open-class words are symmetrical or larger over the right than the left.

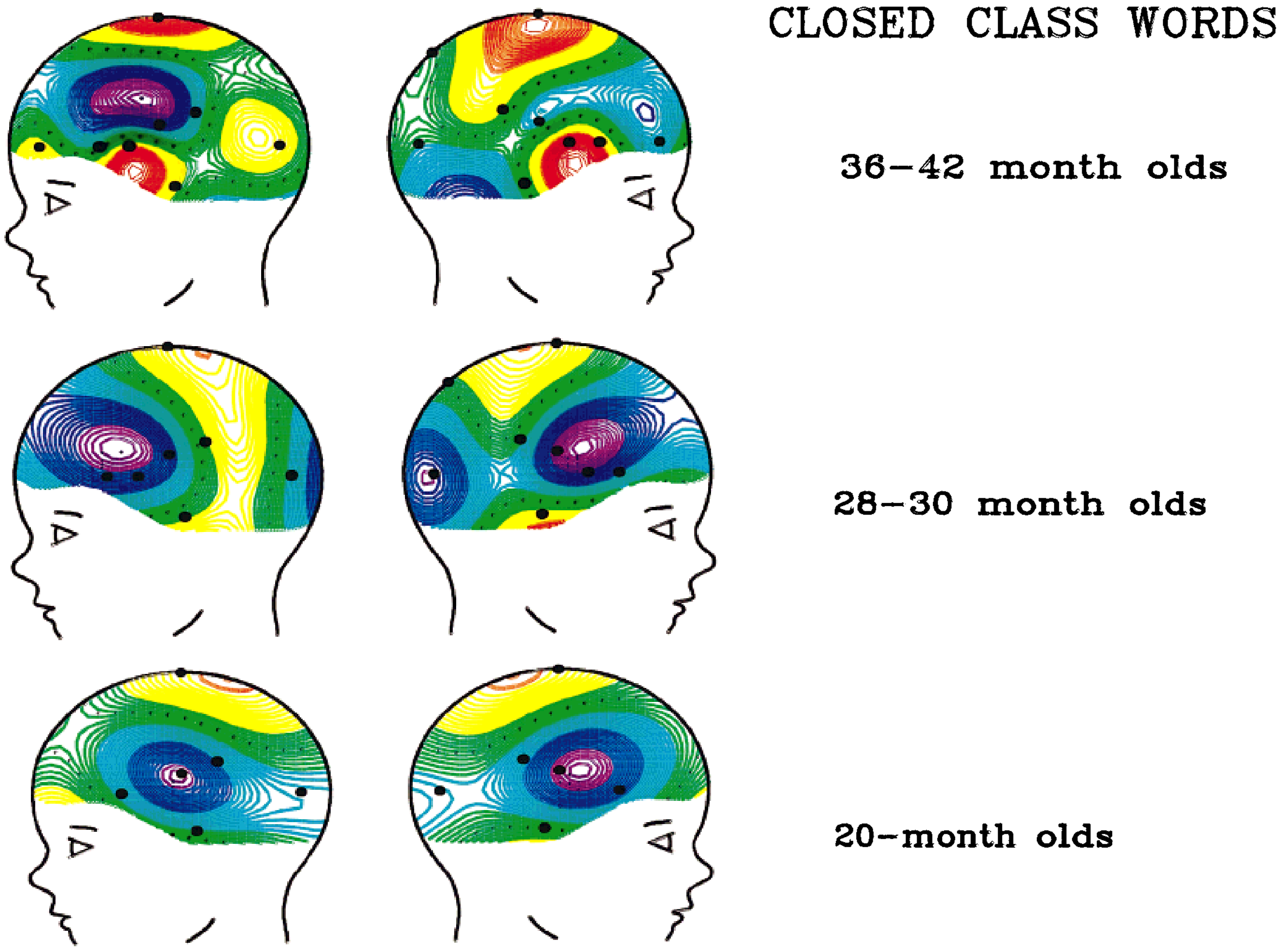

Fig. 7. Current source density (CSD) analyses of neural activity to closed-class words at 200 msec. The CSDs illustrate sinks, i.e., activity flowing into the head (purple), and sources, i.e., activity flowing out of the head (orange), at three age groups. Top: At 36–42 months the CSD shows a sink over left anterior regions. Middle: At 28–30 months the CSD show sinks that are bilateral but slightly more prominent over the right than the left hemisphere. Bottom: At 20 months the CSD shows sinks over both the left and the right hemispheres.

stimuli were matched for length and volume.

Forward vs. backward words

One of the first things we were interested in was whether ERPs to words would be discriminated from nonwords. Figure 4 shows that ERPs to forward and backward words were different by at least 150–200 ms after word onset even in the youngest group (6 months) and this pattern was observed through adulthood. For infants and young children, ERPs to forward words were characterized by a positive component at 100 ms (P100), two negative peaks at approximately 200 and 350 ms, and a broad negative component from 600–900 ms. The N200 and N350 were absent or attenuated to backward words across all ages. Marked changes in the morphology, latencies, and distributions of ERPs to familiar words were observed with increasing age [Fig. 4; see also Neville, 1995; Mills and Neville, 1997]. The latencies of all components decreased with increasing age, whereas the amplitudes of the components linked to word meaning increased over temporal and parietal regions.

Known vs. unknown words

Of particular interest was whether ERPs to words whose meanings were understood would be different from ERPs to words whose meanings were not understood. Moreover, would ERP differences to known and unknown words change with increasing age and the attainment of new language milestones? During the second year of life, children undergo a dramatic change in their ability to understand and produce words. Typically, between 13 and 20 months children show a marked increase in the number of words they produce—the ‘‘vocabulary spurt.’’ In these studies, we examined changes in the organization of brain activity linked to language comprehension in children from ages 13–20 months, i.e., before and after the vocabulary spurt [Mills et al., 1993, 1997]. At 13–17 months, the period before the vocabulary spurt, ERPs to known words were different from those to unknown words by 200 ms after word onset (Fig. 5, top). The N200 and 350 were larger to known than unknown words. These differences were broadly distributed and were observed over frontal, temporal, parietal, and occipital regions of both the left and right hemispheres. In contrast, by 20 months of age, after the vocabulary spurt, these ERP differences were limited to temporal and parietal regions of the left hemisphere (Fig. 5, bottom). These data suggest that there are marked increases in the functional specialization of the neural systems mediating language comprehension from 13–20 months of age.

To investigate the hypothesis that these changes were linked to increasing

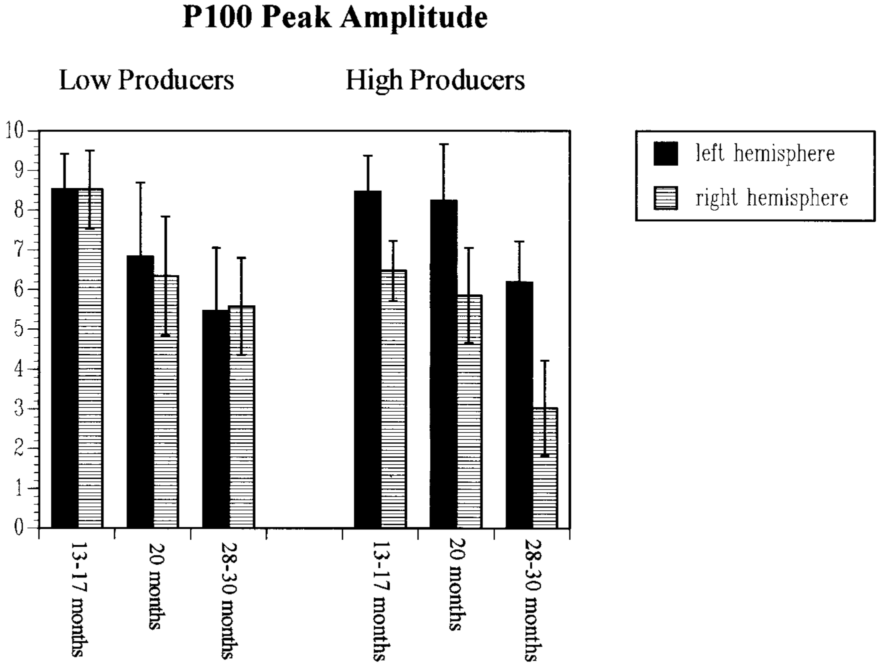

Fig. 8. Mean amplitudes of the P100 over temporal and parietal regions for high and low producers over the left and right hemispheres. Low producers (left) show symmetrical P100 responses at each age group. High producers (right) show left greater than right P100 responses at each age group.

language abilities, the children in each age group were divided into two groups, based on vocabulary size (as measured by the MacArthur Communicative Development Inventory [CDI], a normed parental report measure). At both age groups, children with larger vocabularies, i.e., above the 50th centile, showed a more focal distribution of ERP differences to known and unknown words than did children with smaller vocabularies. These results suggest that some aspects of brain organization may be linked to language experience independently of chronological age.

Does increasing specialization in cerebral organization occur as a function of experience with individual words or as a function of increasing experience with language in general? That is, do the neural processes become more specialized, i.e., more automatic, with repeated exposure to individual words or are new words acquired in a qualitatively different way before and after the vocabulary spurt [as has been suggested by behavioral research, Dore, 1978; McShane, 1979; Gopnik and Meltzoff, 1986; Markman, 1991]? In this study, we examined changes in brain activity as 18–20-month-old children learned completely new words [Schafer and Mills, 1997]. In the training condition, novel words were paired with novel objects (‘‘novel-trained’’). Another set of novel words was repeated without being paired with objects to control for the effects of repetition and familiarity with the sound pattern (‘‘novel-not trained’’). The results showed that, as in previous studies, the N200 and N350 to newly acquired words were larger than to novel words that had been repeated but not paired with an object. These results support the hypothesis that the amplitudes of the N200 and N350 are linked to word meaning. The children were divided into two groups based on vocabulary size, i.e., above and below the 50th centile on the CDI. The low producers showed ERP differences to trained vs. not trained novel words that were widely distributed over both hemispheres, i.e., the pattern previously observed for the 13–17-month-olds. In contrast, the high producers showed ERP differences that were limited to the left hemisphere, i.e., like the more mature 20-month-old pattern. These preliminary results are consistent with the hypothesis that cortical activation when learning new words is linked to meaning and to vocabulary size rather than to the amount of exposure to sounds per se.

Semantic vs. grammatical function words

As described above, studies of adults and school-age children suggest that different aspects of language, i.e., semantic and grammatical processes, are mediated by different brain systems that have different developmental trajectories. In this section we examine how these specializations may arise during the course of primary language acquisition as infants acquire different types of words.

Here we compared ERPs to open- and closed-class words in infants and young children from 20–42 months of age (Fig. 6). All children understood and said both the open- and closed-class words presented. At 20 months, ERPs did not differ for open- and closed-class words (Fig. 6, top). However, both open- and closed-class words elicited ERPs that differed from those elicited by unknown and backward words. These data suggest that in the earliest stages of language development, when children are typically speaking in single-word utterances or beginning to put two words together, open- and closed-class words elicit similar patterns of brain activity. At 28–30 months of age, when children typically begin to speak in short phrases, ERPs to open- and closed-class words elicited different patterns of brain activity (Fig. 6, middle). However, the more mature left hemisphere asymmetry to closed-class words was not observed. In contrast, at 28–30 months closed-class words elicited a right greater than left asymmetry. By 3 years of age most children speak in sentences and use closed-class words appropriately to specify grammatical relations and, like adults, ERPs from 3-year-olds displayed a left hemisphere asymmetry to closed-class words. Figure 7 illustrates the development of the left hemisphere asymmetry to closed-class words in current source

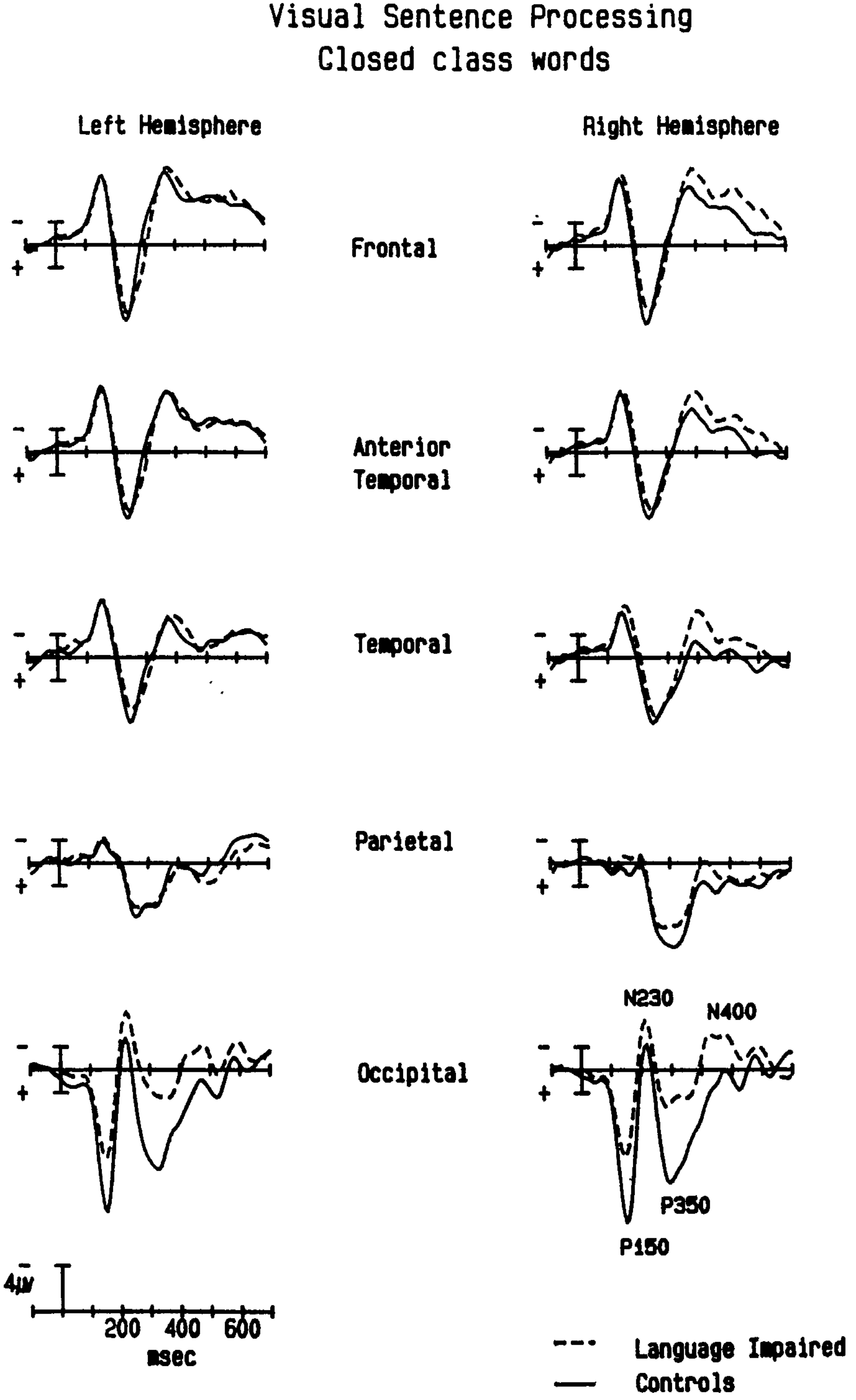

Fig. 9. ERPs to closed-class words in the middle of sentences from left and right frontal, anterior temporal, temporal, parietal, and occipital sites of control and LI children. [Reprinted from Neville et al., 1993 with permission of the publisher.]

density maps across the three age groups. The results across the three groups are consistent with the hypothesis that initially open- and closed-class words are processed by similar brain systems, and that these systems become progressively specialized with increasing language experience.

To further investigate this hypothesis, we examined ERPs in children who were the same age but who differed in language abilities. The 20-month-old high-producers scored above the 50th centile on the CDI, the low producers scored below the 50th centile. The 20-month-old low-producers did not show ERP differences to open- and closed-class words. In contrast, the high producers showed ERP differences to open- and closed-class words that were similar to the 28–30-month-old patterns shown above. We also collected data from 28–30 and 36–42-month-old late talkers [Mills and Neville, 1996]. The late talkers scored below the 10th centile for vocabulary size on the CDI and were identified through the Project in Cognition and Neural Development (PCND) at the University of California at San Diego, in collaboration with Dr. Donna Thal. The 28–30-month-old late-talkers scored in the same range as the 20-month-old low-producers on the CDI. Like their language-matched cohort, the 28–30-month-old late-talkers did not show ERP differences to open- and closed-class words. Similarly, the 36–42-month-old late-talkers showed ERP patterns similar to the 28–30-month-old normal controls. These date strongly suggest that the organization of brain activity is linked to language abilities rather than to chronological age per se.

Predictors of language abilities

In the sections above we described research suggesting that the N200 and N350 were linked to word meaning and that the distribution and responsiveness of these components to different types of words changed with the attainment of new language milestones. In this section, we discuss the lateral distribution of an earlier response in the ERP, the P100, that does not change with increasing vocabulary size or age, at least between 6–28 months, but appears to be predictive of later language abilities. Figure 8 shows P100 amplitudes for three age groups of children, 13–17, 20, and 28–30 months [Mills and Neville, in press]. Within each age group, the children who have large vocabularies display a P100 response that is larger over the left than the right hemisphere. In contrast, the children with small vocabularies display P100 responses that are symmetrical. However, there were individual differences in the late-talker population. Three of the 13 children showed a left greater than right P100 asymmetry to comprehended words. A follow-up study showed that by 36–42 months of age these three children scored within the normal range for both comprehension and production (on the Reynell test). Although the results are preliminary, these data suggest that the presence or absence of a P100 that is larger over the left than right hemisphere may help predict which late talkers may catch up and which are at risk for language impairment.

Language Impairment

Consideration of the several different types of processing that interact in the comprehension and production of language and of the multiple different time periods during which these systems may be dependent on environmental input for their normal development raises the strong likelihood that impairments of language might arise from internal or environmentally determined deficits within any one of a number of different systems.

In studies of language impaired (LI) children ages 9–12 years, we observed that some children displayed deficits in processing non-language auditory information while others did not. Other LI children displayed abnormalities within the earliest stages of visual processing but not within auditory processing. Others displayed abnormal ERP responses in response to the grammatical information provided in closed-class words but no evidence of auditory sensory processing deficits [Neville et al., 1993] [Fig. 9].

The visual processing deficits displayed by some LI children may be linked to the apparently greater developmental vulnerability of the (dorsal) visual pathway important in processing transient visual information [Neville et al., 1993; Neville, 1995; Lovegrove et al., 1986; Eden, et al., 1996]. A similar differential vulnerability may exist in the auditory system [Galaburda, 1994]. The vulnerability of grammatical processing in LI children is consistent with the results for bilingual and deaf adults (reported above). By contrast, other aspects of processing are intact in LI children. Further research is necessary to investigate the hypothesis that language impairment is a final similar, but not identical, result that can arise from the vulnerability of any one of many different systems important in language.

In summary, children do not begin processing language using the same systems as adults, but if language experience occurs in the normal, early fashion the hallmark specialization of the left hemisphere develops within the first few years of life. Virtually all adults, hearing or deaf, processing their native language, spoken or signed, display activation within anterior regions of the left hemisphere. This aspect of neural development is strongly determined. Nonetheless, if language learning is delayed, as in the case of late bilinguals (hearing and deaf), this strongly determined aspect of functional organization does not develop. This pattern is characteristic of development within many other systems, including vision (e.g., in the formation of ocular dominance columns and depth perception) and within audition (e.g., in the development of sound localization based on binaural input). Future research is necessary to understand why certain aspects of neural development within different systems are epigenetically constrained in this way and while other can be modified throughout life. ■

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