

THE NEW COGNITIVE NEUROSCIENCES

Second Edition

Michael S. Gazzaniga, *Editor-in-Chief*

Section Editors: Emilio Bizzi
Ira B. Black
Colin Blakemore
Leda Cosmides
Gregory J. DiGirolamo
Stephen M. Kosslyn
Joseph E. LeDoux
Willem J. M. Levelt
J. Anthony Movshon
Michael I. Posner
Pasko Rakic
Daniel L. Schacter
Edward E. Smith
John Tooby
Endel Tulving

A BRADFORD BOOK
THE MIT PRESS
CAMBRIDGE, MASSACHUSETTS
LONDON, ENGLAND

Reprinted with permission of the publisher via
the Copyright Clearance Center, Inc.

7

Specificity and Plasticity in Neurocognitive Development in Humans

HELEN J. NEVILLE AND DAPHNE BAVELIER

ABSTRACT Brain imaging studies of adults who have had altered sensory and language experience and studies of normally developing children during sensory and language processing tasks are summarized. The results suggest that different subsystems within vision and within language display different degrees of experience-dependent modification of cortical organization. Within vision, the organization of systems important in processing peripheral space and motion information is most altered following auditory deprivation. Within language, delayed exposure to a language has pronounced effects on the development of systems important in grammatical processing, and has many fewer effects on lexical development. Hypotheses concerning the origins of these differential effects of early experience are discussed.

Cognitive neuroscience has rapidly expanded during the decade of the brain. Progress in cognitive science and in the development of techniques that permit noninvasive monitoring of the human brain have permitted extensive, ongoing mapping and differentiation of sensory and cognitive systems in the mature human mind/brain. The burgeoning literature on the normal adult brain serves as the point of departure for a major opportunity and challenge for the coming decade and century—the characterization of the processes that lead to the development and differentiation of the mature brain (developmental cognitive neuroscience).

Discussions of neurocognitive development have long been dominated (and stifled) by the “nature–nurture” debate. Most current investigators acknowledge both the role of biological constraints imposed by the genotype and the role of environmental inputs in gene expression and other chemical and physiological developmental events. It is clear that neurocognitive development relies on a dynamic and complex interplay between predetermined genetic events and environmental events. In this chapter we argue that the degree of interplay is highly

variable across different neurocognitive systems, leading to different degrees and timing of sensitivities to environmental inputs for different brain functions. These differences in developmental specificity and plasticity prevent simple generalization and call for a careful characterization of the developmental events within each system and subsystem.

This chapter offers (1) evidence on the development of the anatomy of the developing cerebral cortex in humans; (2) a review of developmental plasticity of higher visual functions, considering separately functions of the ventral and dorsal visual pathways; (3) a brief discussion of reports on plasticity within the development of other sensory systems; and (4) a consideration of developmental plasticity and specificity of language functions with an emphasis on the comparison of lexical and grammatical functions.

Anatomy and physiology of the developing human brain

Although a thorough review of the structural, chemical, and physiological development of the human brain is beyond the scope of this chapter, this section aims at summarizing the state of knowledge on postnatal human development from infancy to adulthood.

In most species, including humans, the developing brain displays progressive and regressive events during which axons, dendrites, synapses, and neurons show exuberant growth and major loss leading to a remodeling of the neural circuitry. This period of remodeling is hypothesized to be a time during which environmental factors can have a major impact on cortical organization. Several studies of primary sensory areas have shown that sensory inputs are of central importance in selecting the axons, dendrites, synapses, and neurons that form functional neural circuits (Rakic, 1976; Hubel and Wiesel, 1977; Sur, Pallas, and Roe,

HELEN J. NEVILLE University of Oregon, Eugene, Ore.
DAPHNE BAVELIER University of Rochester, Rochester, N.Y.

1990). For example, during a specific time period (the sensitive period), visual deprivation induced by monocular eyelid suture results in shrinkage of ocular dominance columns serving the closed eye. Outside the critical period, visual deprivation has little effect on the pattern of ocular dominance (Blakemore, Garey, and Vital-Durand, 1978; Hubel and Wiesel, 1977; Horton and Hocking, 1997). Little is known about the factors that control the duration and timing of sensitive periods; however, the onset of the sensitive period is affected by input. For example, in cats, binocular deprivation results in delayed onset of the sensitive period for ocular dominance formation (Cynader and Mitchell, 1980; Mitchell, 1981). Similar observations have been made in the auditory system of songbirds (Marler, 1970) and humans. The maturation of an early auditory evoked response displays an extended time course of development after cochlear implantation in congenitally deaf children (Ponton et al., 1996). The number of years of auditory experience, rather than chronological age per se, was predictive of the maturational time course.

Different neural systems and associated behavioral capabilities are affected by environmental input at highly variable time periods, supporting the idea that they develop along distinct time courses (Mitchell, 1981; Harwerth, et al., 1986; Curtiss, 1989; Neville, Mills, and Lawson, 1992; Maurer and Lewis, 1998). For example, visual processes thought to arise within the retina (cf. the sensitivity of the scotopic visual system) display relatively short sensitive periods. By contrast, binocular functions that rely on later developing cortical neurons display considerably longer sensitive periods (Harwerth et al., 1986). This variability in the timing of experience-dependent modification may depend upon the rate of maturation of the neural systems that mediate different functions, with later developing cortical areas having more opportunity to be affected by incoming input.

The proposal that different brain systems in the human display distinct developmental time courses is supported by anatomical and physiological measurements. Recently developed neuroanatomical techniques can be used to provide estimates of the density of neurons, axons, dendrites, or synapses in tissue. Huttenlocher and collaborators (Huttenlocher, 1994; Huttenlocher and Dabholkar, 1997) have used electron microscopy to map out the synaptic remodeling that occurs during human development. These authors have compared synaptogenesis and synapse elimination within several different brain areas (Huttenlocher, 1994). In primary visual cortex a burst in synaptogenesis occurs at about 3 to 4 months of age, with the maximum density reached at 4

months. In contrast, synaptogenesis in the middle prefrontal cortex takes longer, reaching a maximum synaptic density at about 3.5 years of age. Furthermore, the time course for synapse elimination occurs significantly later in the middle frontal gyrus (until age 20) than in the primary visual cortex (converged on adult levels by age 4; see figure 7.1; Huttenlocher and Dabholkar, 1997). Recently, Huttenlocher and colleagues have described developmental changes in synaptic density for different cortical areas important in language processing—primary auditory cortex, the angular gyrus (Brodmann's area 40), and Broca's area (Huttenlocher, 1994; Huttenlocher and Dabholkar, 1997). At birth synaptic development (as measured by the time course of synaptic density) in the auditory cortex is more advanced than in the two language areas; but by 4 years of age, synaptic density is similar in these areas and is significantly greater than in the adult (by about a factor of 2). These findings suggest different time courses of synaptogenesis for different brain systems. A recent report suggests there may also be considerable postnatal variability in neuron loss and neurogenesis in the human brain (Shankle et al., 1998b). However, other neuroanatomic features of the human brain appear to show concurrent developmental patterns from region to region (Shankle et al., 1998a). In macaque monkeys, Rakic and colleagues (1986) have reported concurrent time courses of synaptogenesis across several different brain areas. However, there is variability between areas in the duration of the maximum densities of synapses, in the elimination phases, and in the timing of synaptogenesis on dendritic shafts and spines (see chapter 4 of this volume).

Anatomical measures of synapse proliferation in the human brain (Huttenlocher and Dabholkar, 1997) describe developmental time courses similar to those observed in physiological studies using PET with FDG, a technique that traces glucose metabolism. Chugani and collaborators (1996) have described the patterns of brain glucose utilization during human development. These studies show a rapid rise in cerebral metabolism during infancy, perhaps reflecting the burst of synaptogenesis described in the structural studies. This is followed by a decrease in brain glucose metabolism later in childhood, in much the same time frame as is observed for the loss of synapses. In the metabolic studies, primary sensory and motor cortex, the hippocampal region, and the cingulate cortex have an earlier increase in glucose metabolism than other cortical regions; and the prefrontal cortex is one of the latest structures to show increased glucose metabolism. These structural and physiological findings support the view of different maturational time-tables for distinct brain structures with primary cortices developing before higher association cortices.

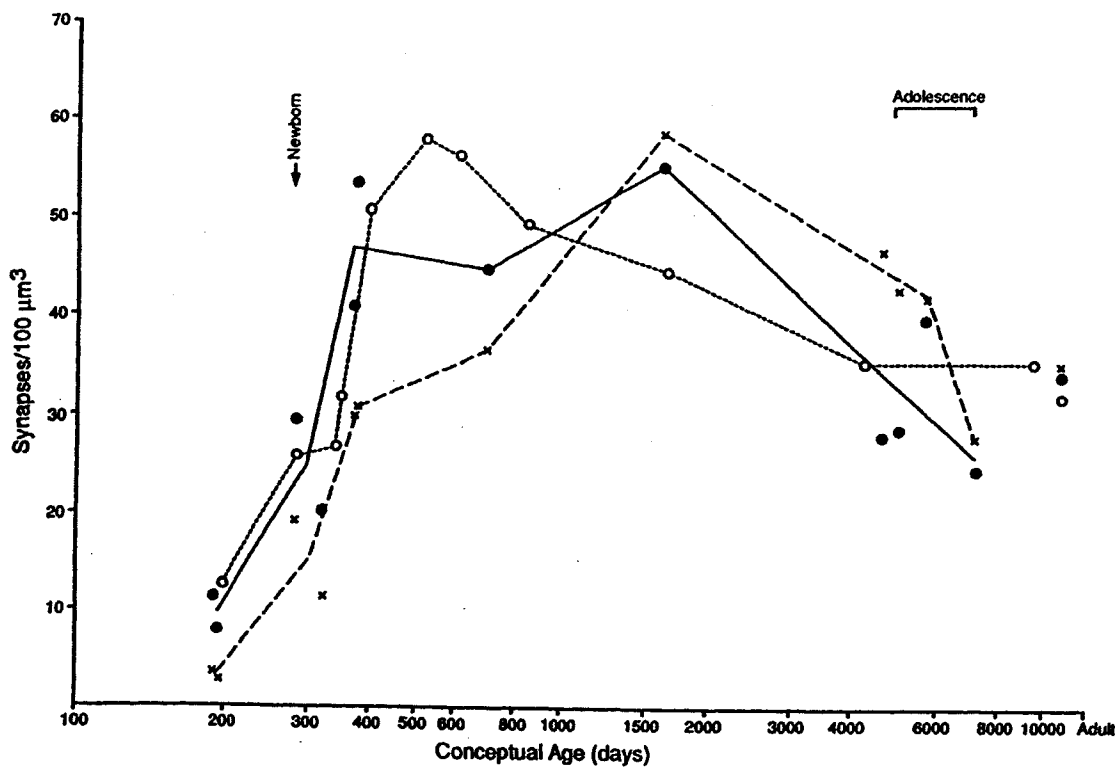


FIGURE 7.1 Mean synaptic density in synapses/100 μm^3 in auditory (filled circles), calcarine (open circles), and prefrontal (x's) cortex at various ages. (Reprinted from Huttenlocher and

Dabholkar, 1997, by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.)

Much more research is necessary to characterize the structural and physiological development of the human brain and to link variability in the development of these parameters to variability in the time course of sensory, motor, and cognitive development in the child.

Developmental specificity of visual functions in humans

We now have powerful brain imaging methods to study aspects of the physiology of sensory and language processing in humans. Event-related brain potentials (ERPs) and functional magnetic resonance imaging (fMRI) are two such techniques. ERPs are voltage fluctuations in the EEG in response to a controlled stimulus. The latencies of different positive and negative components in an ERP reveal the time course of activation (within microseconds) of the neuronal populations that are recruited during the processing of that stimulus. The fMRI technique measures changes in blood flow and oxygenation, permitting mapping of brain regions metabolically active following the presentation of a controlled stimulus. In contrast to the ERP, this technique has a good spatial resolution (about 1 mm) but a restricted temporal resolution.

DORSAL AND VENTRAL VISUAL SUBSYSTEMS In several experiments employing ERPs, we have observed that sensory and attentional processing of visual information presented to the central and peripheral visual fields elicit activity in different neural pathways in normal hearing subjects. Congenital auditory deprivation is associated with specific enhancements of behavioral performance and ERPs in response to visual information presented in the peripheral (but not the foveal) visual fields (Neville, Schmidt, and Kutas, 1983; Neville and Lawson, 1987a, b, c). These data suggest that the systems mediating the representation of peripheral visual space may be more modifiable than those representing central visual space. There is anatomical evidence that the visual periphery is represented most strongly along the dorsal visual pathway that projects from V1 toward the posterior parietal cortex and includes areas important for the processing of spatial location and motion information. By contrast, central space is largely represented along the ventral pathway that projects from V1 to anterior regions of the inferior temporal lobe and includes areas important for processing form and color information (Ungerleider and Mishkin, 1982; Baizer, Ungerleider, and Desimone, 1991). These results prompted the

hypothesis that there may be a greater sensitivity to altered experience for other dorsal visual pathway functions.

In order to investigate this hypothesis, we employed stimuli designed to selectively activate either the magnocellular system (M stimuli) which projects strongly to the dorsal pathway, or the parvocellular system which projects strongly (but not solely: see Stoner and Albright, 1993; Sawatari and Callaway, 1996) to the ventral pathway (P stimuli). The parvo system is highly responsive to color information and to stimuli of high spatial frequency, while the magno system is highly responsive to motion and to stimuli of low spatial frequency and low contrast (Livingstone and Hubel, 1988; Merigan and Maunsell, 1993).

Stimuli were presented at five different locations including the fovea and 8 degrees from the foveal stimulus in the upper and lower left and right visual fields. The parvo (P) stimuli were isoluminant blue and green high spatial frequency gratings (adjusted for the cortical magnification factor) continuously visible at all locations. ERPs were evoked by a brief change in color; randomly at one location the blue bars changed to red for 100 ms. The magno (M) stimuli consisted of low spatial frequency gratings of light and dark gray bars with a low luminance contrast. The evoking stimulus consisted of the bars at one location (random) moving transversely to the right. Subjects fixated centrally and monitored all locations for the rare occurrence of a black square at one of the locations. We first asked whether ERPs to these different stimuli would provide evidence for the activation of distinct neural systems in normal hearing subjects and then asked whether congenital auditory deprivation would have selective effects on these different aspects of processing (Armstrong et al., 1995; Neville and Bavelier, 1998).

In normal hearing subjects the distribution of the ERPs elicited by the parvo and magno stimuli displayed many similarities, and this may be attributable to the spatial proximity (within 1 cm) of the ventral and dorsal stream areas in humans, as indicated in recent fMRI studies (Serenio et al., 1995; Tootell et al., 1995). On the other hand, there were reliable differences in the activity patterns elicited by the stimuli. Magno stimuli elicited responses that were larger dorsally than were responses to parvo stimuli, consistent with our initial hypotheses. Additionally, both the current source density maps and the grand averaged waveforms demonstrate that, whereas the peripheral M stimuli elicited ERPs largest over cortex contralateral to the field of presentation, the P stimuli evoked a bilateral response. This pattern of results may be attributable in part to the deep ventromedial location of V4 which could generate a bilateral

pattern of activation. Area MT, on the other hand, is located more laterally and would therefore generate a stronger contralateral response. Thus, these differences are consistent with anatomical differences of ventral and dorsal stream areas.

In addition, magno stimuli elicited ERP responses with considerably earlier latencies than those elicited by parvo stimuli, consistent with evidence from animal studies that show faster conduction within the magnocellular pathway. In addition, for several early components (beginning at 110 ms), P stimuli presented in the upper and lower visual fields (VF) evoked different response amplitudes while magno stimuli did not. These results may be accounted for by the retinotopic organization of V4 and MT/MST. fMRI data from humans (Serenio et al., 1995) have shown that upper and lower VF representations in several ventral stream areas including V4 are centimeters apart; however, in areas MT and MST, the representations are adjacent. Thus, a difference in response to parvo stimuli in the upper and lower VF is consistent with ventral stream activation, and the similarity of responses to magno stimuli in the upper and lower VF is consistent with dorsal stream activation. In summary, these stimuli were successful in evoking distinct ERP responses that may index the activation of separate streams or modes of visual processing in normal hearing subjects.

EFFECTS OF AUDITORY DEPRIVATION Our prior research, coupled with evidence that different systems within vision display different developmental time courses and modification by visual experience (Sherman, 1985), led us to hypothesize that processing of the magno stimuli would be selectively enhanced in congenitally deaf subjects.

Subjects were 11 congenitally, profoundly and bilaterally deaf subjects born to deaf parents. Whereas hearing subjects' reaction times were faster to targets occurring in the central than in the peripheral visual field, deaf subjects responded equally quickly to targets in the central and peripheral fields. Several specific group differences occurred in the amplitude and distribution of early sensory responses recorded over anterior and temporal regions. Deaf subjects displayed significantly greater amplitudes than hearing subjects—but this effect occurred only for magno stimuli, not for parvo stimuli (see figure 7.2). Further, whereas in hearing subjects, P stimuli elicited larger responses than did M stimuli, in deaf subjects responses to M stimuli were as large as those to P stimuli. In addition, at 150 ms ERPs to the M stimuli displayed a source-sink generator in temporal cortex that was clearly present in the deaf subjects but not in the hearing subjects. Currently, we are acquiring

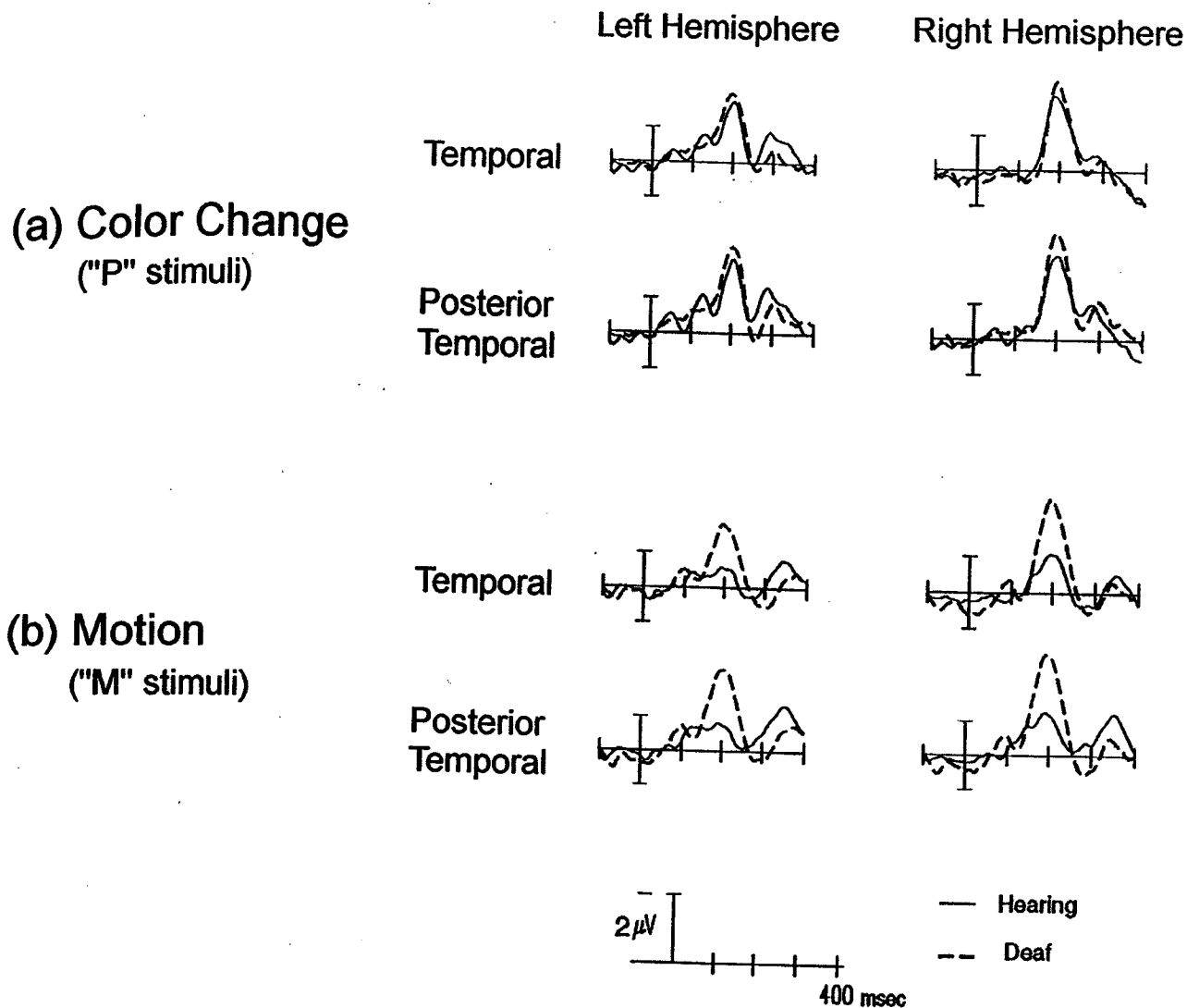


FIGURE 7.2 ERPs elicited by (a) color change and (b) motion in normally hearing and congenitally deaf adults. Recordings from temporal and posterior temporal regions of the left and

right hemispheres. (Reprinted with permission from Neville and Bavelier, 1998.)

results from a group of hearing subjects born to deaf parents who acquired ASL as a first language. This research should allow us to determine whether certain group effects observed in this experiment are attributable to auditory deprivation and others to acquisition of a visuospatial language (ASL) since, in previous research, we have observed separate effects of these two factors (Neville and Lawson, 1987c).

These data suggest that there is considerable specificity in the aspects of visual processing that are altered following auditory deprivation; specifically, the dorsal visual processing stream may be more modifiable in response to alterations in afferent input than is the ventral processing pathway. This hypothesis is in broad agreement with the proposal put forward by Chalupa and Dreher (1991) that components of the visual pathway

that are specialized for high acuity vision exhibit fewer developmental redundancies ("errors"), decreased modifiability, and more specificity than do those displaying less acuity and precision. It may also be that the dorsal visual pathway has a more prolonged maturational time course than the ventral pathway, permitting extrinsic influences to exert an effect over a longer time. While little evidence bears directly on this hypothesis, anatomical data suggest that, in humans, neurons in the parvocellular layers of the LGN mature earlier than those in the magnocellular laminae (Hickey, 1977) and, in nonhuman primates, the peripheral retina is slower to mature (Lachica and Casagrande, 1988; Packer, Hendrickson, and Curcio, 1990; Van Driel, Provis, and Billson, 1990). Additionally, data suggest that the development of the Y-cell pathway (which is strongest in the periphery of

RESPONSES TO SPEECH

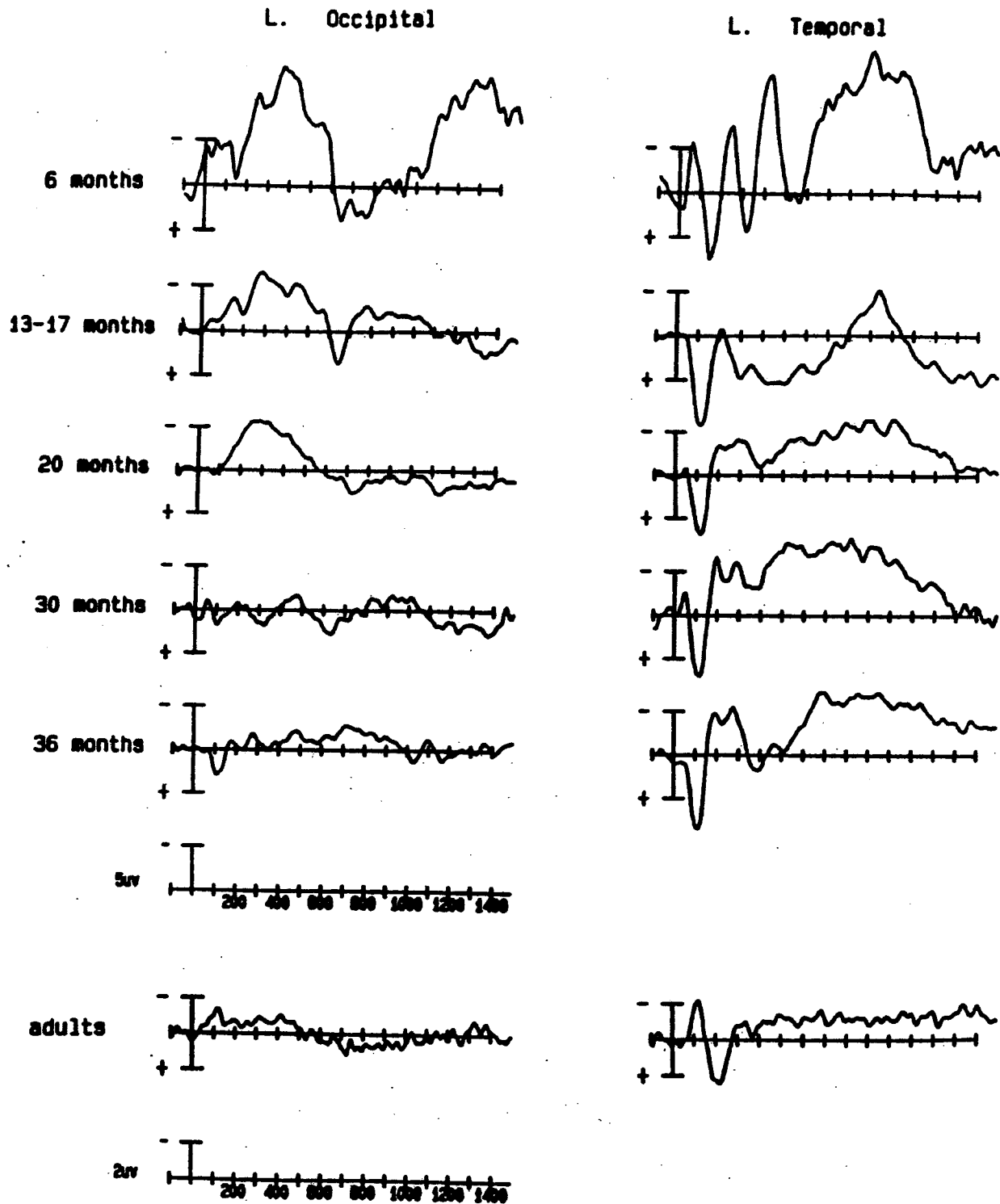


FIGURE 73 ERPs to auditory (speech) stimuli recorded over temporal and occipital regions in normal adults (bottom) and in children aged 6-36 months. (Reprinted with permission from Neville, 1995.)

the retina) is more affected by visual deprivation than is development of the W- and X-cell pathways (Sherman and Spear, 1982). Investigators have also reported that the effects of congenital visual deprivation (due to cataracts) are more pronounced on peripheral than foveal vision (and by implication on the dorsal pathway) (Mioche and Perenin, 1986; Bowering et al., 1997). Moreover, in developmental disabilities including dyslexia, specific language impairment, and Williams syndrome, visual deficits are more pronounced for dorsal than ventral visual pathway functions (Lovegrove, Garzia, and Nicholson, 1990; Eden et al., 1996; Atkinson et al., 1997). An additional hypothesis that may account for the greater effects on peripheral vision is that in development the effects of deprivation and enhancement are equivalent within all cortical regions. Those areas with less extent to begin with (e.g., MT, peripheral visual representations) would display the largest proportional effects of both enhancement and vulnerability. A similar hypothesis has been proposed to account for the larger effects of visual deprivation on ocular dominance formation within the periphery in monkeys (Horton and Hocking, 1997).

SENSITIVE PERIOD EFFECTS AND MECHANISMS We have observed that individuals who became deaf after the age of 4 years (due to delayed expression of the gene that leads to cochlear degeneration) typically do not display the increased visual ERPs that we attributed to auditory deprivation (Neville, Schmidt, and Kutas, 1983; Neville and Lawson, 1987c). We considered several mechanisms that might mediate the effects themselves and the developmental time limits on them. One possibility is that they are mediated by an early, normally transient, redundancy of connections between the auditory and visual systems (as has been observed in cats and hamsters: see Dehay, Bullier, and Kennedy, 1984; Frost, 1984; Innocenti and Clarke, 1984). In the absence of competition from auditory input, visual afferents may be maintained on what would normally be auditory neurons. Our results from studies of later deafened individuals suggest that in humans this redundancy may diminish by the fourth year of life. One way we tested this hypothesis was to study the differentiation of visual and auditory sensory responses in normal development (see figure 7.3). In normal adults, auditory stimuli elicit ERP responses that are large over temporal brain regions but small or absent over occipital regions. By contrast, in 6-month-old children we observed that auditory ERPs are equally large over temporal and visual brain regions, consistent with the idea that there is less specificity and more redundancy of connections between auditory and visual cortex at this time. Between 6 and 36 months, however, we ob-

served a gradual decrease in the amplitude of the auditory ERP over visual areas, while the amplitude over the temporal areas was unchanged. These results suggest that early in human development there exists a redundancy of connections between auditory and visual areas and that this overlap gradually decreases between birth and 3 years of age. This loss of redundancy may be the boundary condition that determines when auditory deprivation can result in alterations in the organization of the visual system. Ongoing studies of hearing and deaf infants and children employing the parvo and magno stimuli described above will test for the specificity of these effects.

fMRI STUDY OF MOTION PERCEPTION We have further pursued the hypothesis that deafness alters the functional organization of the dorsal visual stream, by employing fMRI (Tomann et al., 1998). Specifically, we assessed whether early auditory deprivation alters cerebral activation during motion processing. In addition, we hypothesized that these changes would be most marked when visual attention was required in view of the central role of dorsal parietal regions in spatial attention. Motion processing was compared between congenitally deaf (native signers/born to deaf parents) and hearing individuals as visual attention was manipulated. Subjects fixated centrally and viewed an alternation of radial flow fields (converging and diverging) and static dots. While the first run required only passive viewing, visual attention was manipulated in all other runs by asking subjects to detect velocity and/or luminance changes.

Under conditions of active attention, deaf individuals showed a greater number of voxels activated and a larger percent signal change than did hearing subjects in temporal cortex including areas MT-MST (figure 7.4; see color plate 1). Thus, congenital deafness alters the cortical organization of motion processing, especially when attention is required. Interestingly, the recruitment of the intraparietal sulcus was also significantly larger in deaf than in hearing subjects. This result, like our earlier ERP study of spatial attention (Neville and Lawson, 1987b; Neville, 1995), suggests that early auditory deprivation may also alter the cortical organization of visual attention. Ongoing studies will determine the precise location and the specificity of these effects.

Developmental specificity in other neurocognitive domains

Developmental plasticity has also been documented in humans within other sensory modalities. There are several reports that early peripheral blindness leads to changes in the visually deprived cortex. Measures of glucose utilization have shown an increased metabolism

MOTION RELATED ACTIVATION MONITOR BRIGHTNESS CHANGES

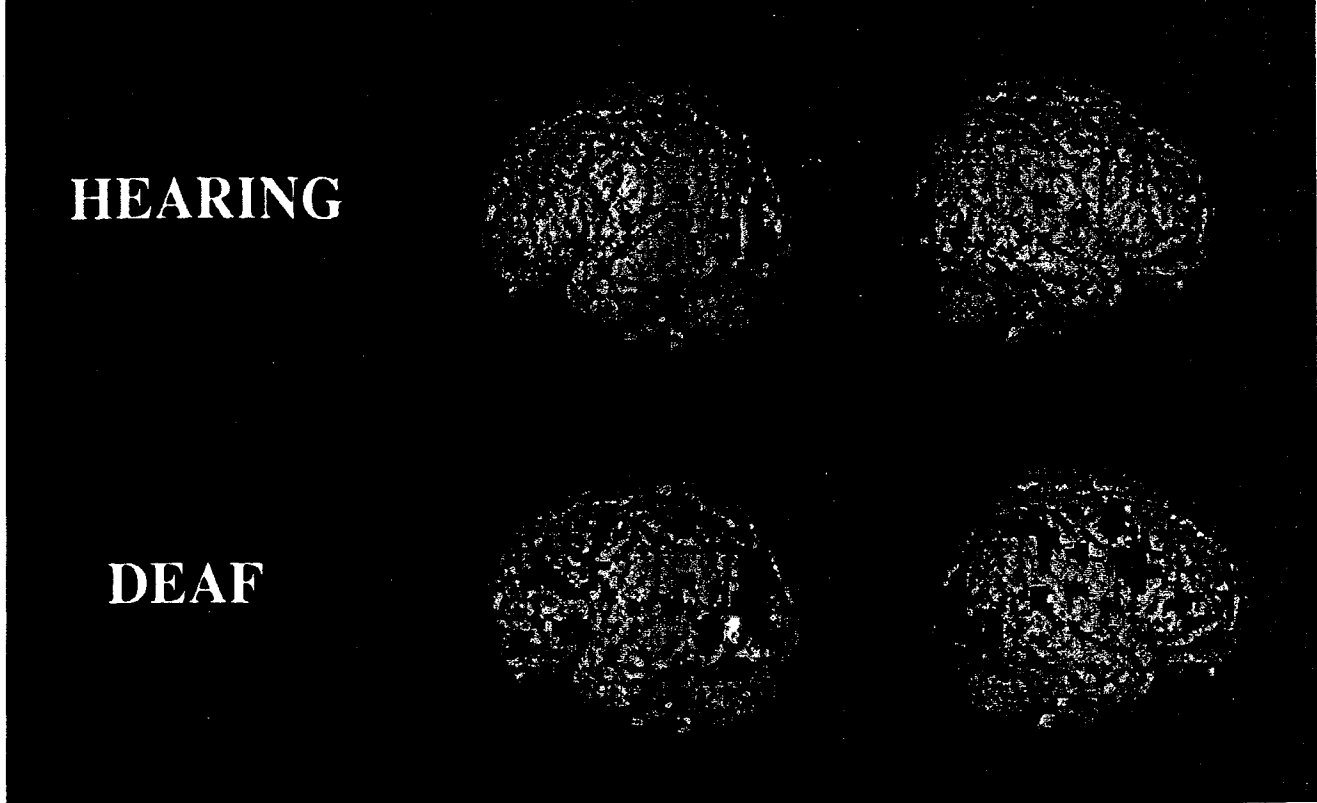


FIGURE 7.4 Activation (fMRI, 1.5T) in normally hearing and congenitally deaf adults in response to visual motion.

in the visual cortex of early blind humans as compared to subjects who became blind after the completion of visual development. These studies report that metabolic activity within the occipital cortex of early blind individuals is higher than that found in blindfolded sighted subjects and equivalent to that of sighted subjects with their eyes open (Wanet-Defalque et al., 1988; Veraart et al., 1990; Uhl et al., 1994). Additionally, ERP studies indicate a larger slow negative DC potential shift over the occipital lobe in early blind than in sighted persons during tactile and auditory tasks (Uhl et al., 1991, 1994; Röder et al., 1996, 1997). Recently, a number of studies have confirmed the functional participation of visual areas during somatosensory tasks in early blind individuals. Using PET, Sadato and colleagues (Sadato et al., 1996) compared tactile discrimination in early blind braille readers and control subjects. Blind subjects revealed activation of visual cortical areas whereas these regions were deactivated

in controls. The functional relevance of visual areas in tactile discrimination was further established in a transcranial magnetic stimulation experiment (Cohen et al., 1997). Transient stimulation of the occipital cortex induced errors on a tactile task in early blind subjects but had no effect on the sighted controls. It is worth noting that not all aspects of somatosensory processing recruit visual areas in blind subjects. For example, simple tactile stimuli that did not require discrimination produced little activation in visual areas of blind subjects (Sadato et al., 1996). This finding is in agreement with the hypothesis that different neurocognitive systems and subsystems exhibit different sensitivities to altered experience.

This point is further supported by the research of Röder and colleagues (1997) who have studied auditory localization abilities in blind humans. ERPs were recorded as congenitally blind adults and sighted controls attended either to central or peripheral sound sources in

order to detect a rare noise burst either at the 0- or the 90-degree loudspeaker (on different blocks). Behavioral data revealed a higher spatial resolution in the blind, particularly when they were attending to the periphery. Gradients of ERP amplitudes suggested a sharper auditory spatial attention focus in the blind compared to the sighted for peripheral sounds. The results suggest that across auditory and visual modalities the representation of peripheral space is more altered by early sensory experience than is the representation of central space. It is interesting that, on close examination of the behavioral data presented in Rice (1965) on blind humans and Rauschecker and Kneipert (1993) on blind cats, a similar effect is observed—i.e., an advantage in sound localization for the blind that is largest at peripheral locations.

Developmental specificity of language functions in human

It is reasonable to assume that the rules and principles that govern the development of the sensory systems also guide the development of language-relevant brain systems. Thus, differences in the rate of differentiation and degree of specification may be apparent within language and help to identify different functional subsystems. In a series of experiments we have 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 lexical/semantic information elicit a 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 (Neville, Mills, and Lawson, 1992; Nobre and McCarthy, 1994). In addition, sentences that are semantically nonsensical (but grammatically intact) elicit a different pattern of ERPs than do sentences that contain a violation of syntactic structure (but leave the meaning intact) (Neville et al., 1991; Osterhout, McLaughlin, and Bersick, 1997). These results are consistent with several other types of evidence suggesting that 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 lexical/semantic processing and for frontal-temporal systems within the left hemisphere in grammatical processing. 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. Nonetheless, it is likely that language-relevant aspects of cerebral organization are dependent on and modified by language experience. Many investigators have studied this question by comparing cerebral organization in individuals who learned a second language at different times in development (Perani et al., 1996; Dehaene et al., 1997; Kim et al., 1997). In general, age of exposure to language appears to affect cerebral organization for that language. Moreover, there appears to be specificity in these effects: 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 active in lexical/semantic processing. In contrast, delays of just 4 years had significant effects on those aspects of brain organization linked to grammatical processing (figure 7.5; see color plate 2) (Weber-Fox and Neville, 1996). These results and parallel behavioral results from the same study suggest that aspects of semantic and grammatical processing differ markedly in the degree to which they depend upon language input. Specifically, grammatical processing appears more vulnerable to delays in language experience.

STUDIES OF DEAF ADULTS Further evidence on this point was provided by ERP studies of English sentence processing by congenitally deaf individuals who learned English late and as a second language (American Sign Language or ASL was the first language of these subjects; Neville, Mills, and Lawson, 1992). Deaf subjects displayed ERP responses to nouns and to semantically anomalous sentences in written English 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 lexical/semantic processing are largely unaffected by the many aspects of language experience that differ between normally hearing and congenitally deaf individuals. By contrast, deaf subjects displayed aberrant ERP responses to grammatical information like that presented in function words in English. Specifically, they did not display the specialization of the anterior regions of the left hemisphere characteristic of native hearing/speaking learners. These data suggest that the systems mediating the processing of grammatical information are more modifiable and vulnerable in response to altered language experience than are those associated with lexical/semantic processing.

STUDIES OF ASL Recently, we have employed the ERP and fMRI techniques to pursue this hypothesis further and also to obtain evidence on the question of whether the strongly biased role of the left hemisphere

PHRASE STRUCTURE 300 - 500 msec

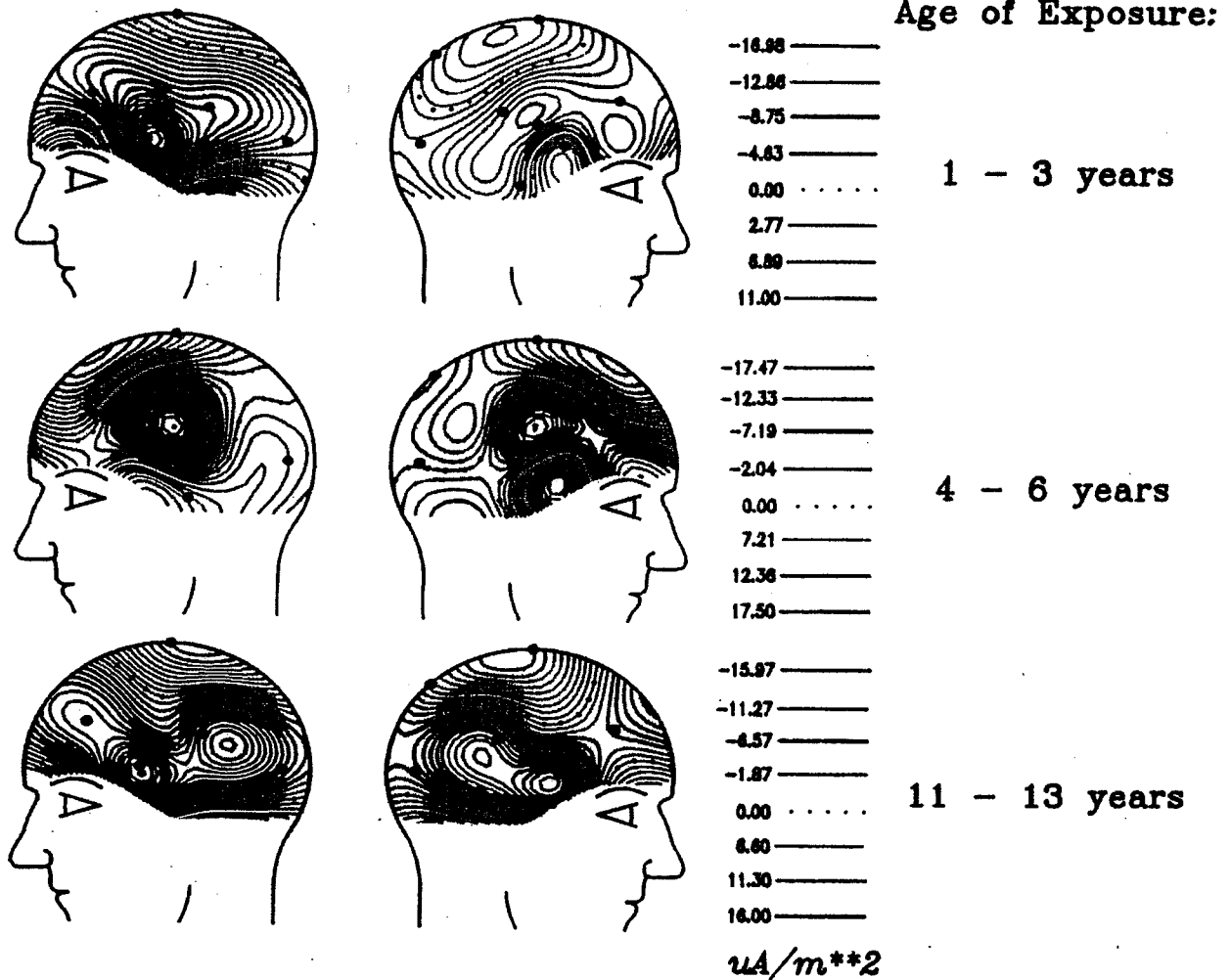


FIGURE 7.5 Current source density (CSD) analyses of responses to grammatical anomalies (violations of phrase structure) in English. Early learners of English (1-3 years) display a

left lateralized activation, but delays in age of exposure (4-13 years) are associated with bilateral activation.

in language occurs independently of the structure and modality of the language first acquired (Neville et al., 1997, 1998). ERPs recorded to response to open- and closed-class signs in ASL sentences displayed similar timing and anterior/posterior distributions to those observed in previous studies of English. But, whereas in native speakers of English responses to closed-class English words were largest over anterior regions of the left hemisphere, in native signers closed-class ASL signs elicited bilateral activity that extended posteriorly to include parietal regions of both the left and right hemispheres. These results imply that the acquisition of a language that relies on spatial contrasts and the perception of motion may result in the inclusion of right-hemisphere regions into the language system. As seen in figure 7.6, both hearing and deaf native signers displayed this effect. However, hearing people who ac-

quired ASL in the late teens did not show this effect, suggesting there may be a limited time (sensitive) period when this type of organization for grammatical processing can develop. By contrast, the response to semantic information was not affected by age of acquisition of ASL, in keeping with the results from studies of English suggesting that these different subsystems within language display different degrees of developmental plasticity.

In fMRI studies comparing sentence processing in English and ASL we also observed evidence for biological constraints and effects of experience on the mature organization of the language systems of the brain. As seen at the top of figure 7.7 (color plate 3), 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.

Closed Class Signs

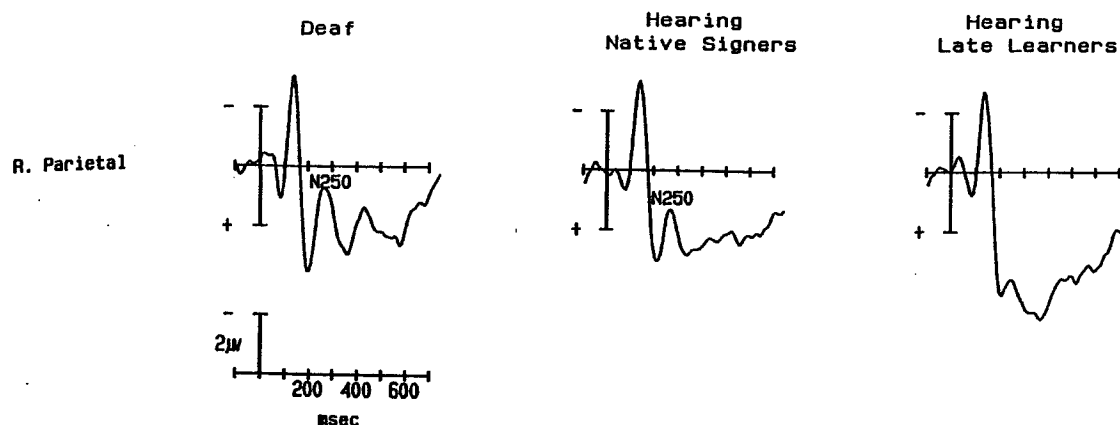


FIGURE 7.6 ERPs to closed-class signs in ASL sentences from 10 deaf, 10 hearing native signers, and 10 late learners of ASL. Recordings from parietal areas of the right hemisphere.

When deaf people read English (their second language, learned late and imperfectly), we did not observe activation of these regions within the left hemisphere (figure 7.7, middle). Is the absence 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 (figure 7.7, bottom). These data suggest a strong biological bias for these neural systems to mediate grammatical 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 described in developmental biology.

The fMRI data also indicate a robust role for the right hemisphere in processing ASL. These results suggest that the nature of the language input, in this case the co-occurrence of location and motion information with language, shapes the organization of the language systems of the brain. Further research is necessary to specify the different times in human development when particular types of input are required for optimal development of the many systems and subsystems important in language processing.

EFFECTS OF PRIMARY LANGUAGE ACQUISITION ON CEREBRAL ORGANIZATION The research summarized above implies that language experience determines the development and organization of language-relevant systems of the brain. A strong test of this hypothesis would be to chart the changes in brain organization as children acquire primary language, and to separate these from more general maturational changes (Mills, Coffey-Corina, and Neville, 1993, 1997; Neville and Mills, 1997). We compared patterns of neural activity relevant to language processing in 13- and 20-month-old infants to determine whether or not changes in cerebral organization occur as a function of specific changes in language development when chronological age is held constant. ERPs were recorded as children listened to a series of words whose meaning was understood by the child, words whose meaning the child did not understand, and backward words. Specific and different ERP components discriminated comprehended words from unknown and from backward words. Distinct lateral and anterior-posterior specializations were apparent in ERP responses to the different types of words. At 13 months of age the effects of word comprehension were apparent over anterior and posterior regions of both the left and right hemispheres. However, at 20 months of age the effects occurred only over temporal and parietal regions of the left hemisphere. This increasing specialization of language-relevant systems is not, however, solely dependent on chronological age. In comparisons of children of the same age who differ in size of vocabulary it is clear that language experience/knowledge is strongly predictive of the maturity of cerebral organization: 13-month-

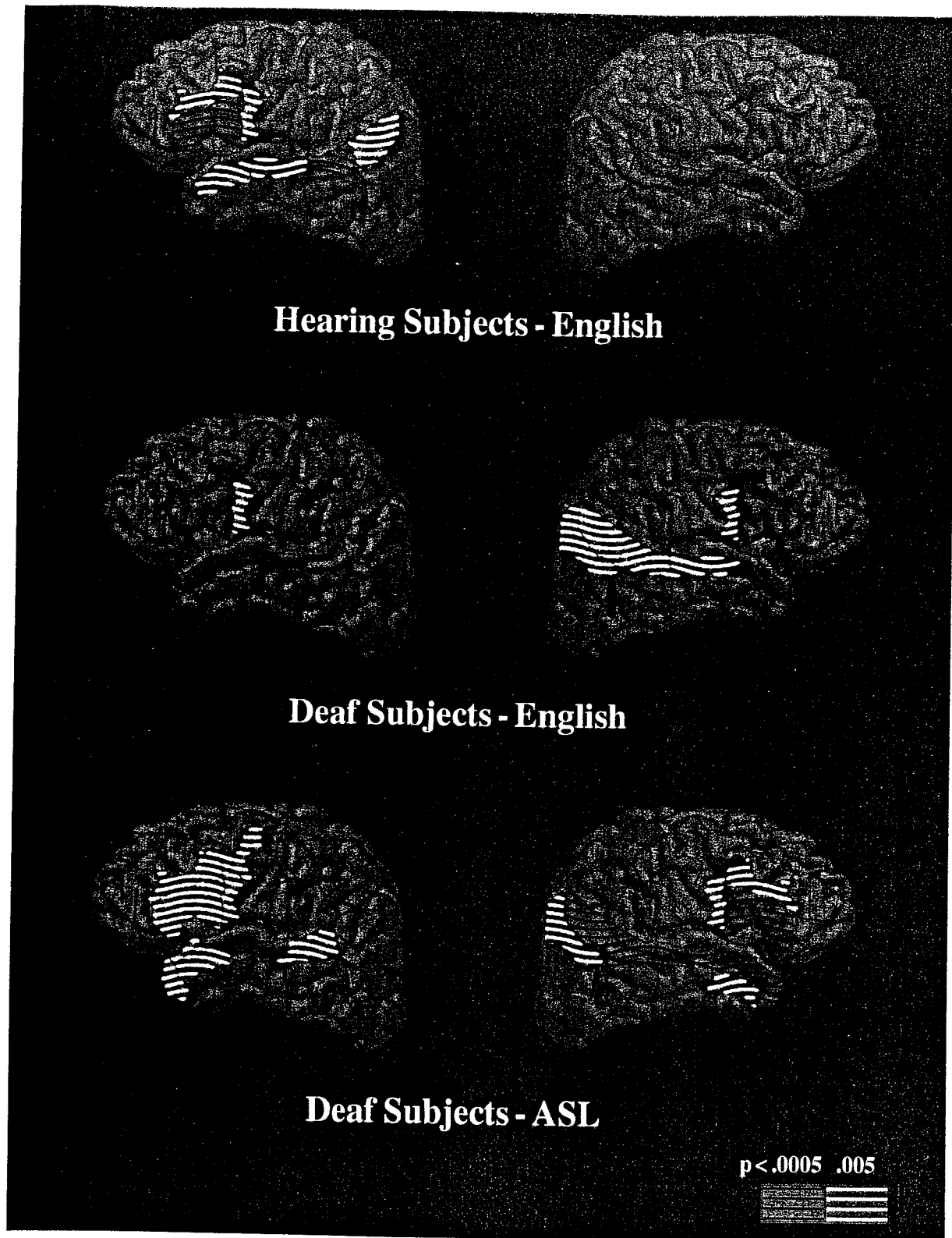


FIGURE 7.7 Cortical areas showing increases in blood oxygenation on fMRI when normal hearing adults read English sentences (top), when congenitally deaf native signers read En-

glish sentences (middle), and when congenitally deaf **native** signers view sentences in their native sign language (American Sign Language).

old infants with large vocabularies also display more focal left temporal/parietal effects of word meaning than do those with small vocabularies.

A similar effect is found in the development of the differential processing of open- and closed-class words. We compared ERPs to open- and closed-class words in infants and young children from 20 to 42 months of age. All children understood and produced both the open- and closed-class words presented. At 20 months, ERPs in response to open- and closed-class words did not differ. However, both types of 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. However, the more mature left-hemisphere asymmetry to closed-class words was not observed. 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 7.8 (color plate 4) illustrates the development of the left-hemisphere asymmetry to closed-class words in current source 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. Further evidence on this hypothesis comes from an examination of ERPs from children who were the same age but differed in language abilities. The 20-month-old children who scored below the 50th percentile for vocabulary size did not show ERP differences to open- and closed-

CLOSED CLASS WORDS

20 month olds

28-30 month olds

36-42 month olds

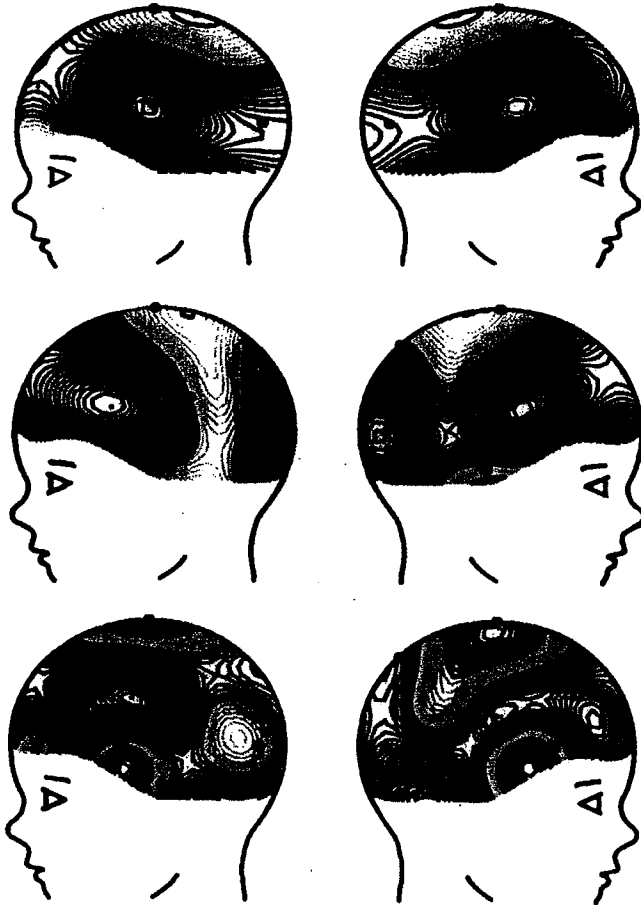


FIGURE 7.8 Current source density (CSD) analyses of neural activity to closed-class words at 200 ms. The CSDs illustrate sinks [i.e., activity flowing into the head (purple)] and sources [i.e., activity flowing out of the head (orange)] at three age groups. Top: At 20 months the CSD shows sinks over both the

left and the right hemispheres. Middle: At 28–30 months the CSD shows sinks that are bilateral but slightly more prominent over the right than the left hemisphere. Bottom: At 36–42 months the CSD shows a sink over left anterior regions.

class words. In contrast, those above the 50th percentile displayed ERP differences to open- and closed-class words that were similar to the patterns shown in 28–30-month-olds. These data strongly suggest that the organization of brain activity is linked to language abilities rather than to chronological age per se.

Summary and conclusions

The results from the language studies, taken as a whole, point to different developmental time courses and developmental vulnerabilities of aspects of grammatical and semantic/lexical processing. They thus provide support for conceptions of language that distinguish these sub-processes within language. Similarly, following auditory deprivation, processes associated with the dorsal visual pathway were more altered than were functions associated with the ventral pathway, providing support for conceptions of visual system organization that distinguish functions along these lines. A general hypothesis that may account for the different patterns of plasticity within both vision and language is that systems employing fundamentally different learning mechanisms display different patterns of developmental plasticity. It may be that systems displaying experience-dependent change throughout life—including the topography of sensory maps (Merzenich et al., 1988; Gilbert, 1995; Kaas, 1995), lexical acquisition (i.e., object–word associations), and the establishment of form, face, and object representations (i.e. ventral pathway functions)—rely upon very general, associative learning mechanisms that permit learning and adaptation throughout life. By contrast, systems important for computing dynamically shifting relations between locations, objects, and events (including the dorsal visual pathway and the systems of the brain that mediate grammar) appear dependent on and modifiable by experience primarily during more limited periods in development. This could account both for the greater developmental deficits and enhancements of dorsal pathway function following various developmental anomalies and for the greater effects of altered language experience on grammatical functions. Further research is necessary to characterize systems that become constrained in this way and those that can be modified throughout life. This type of developmental evidence can contribute to fundamental descriptions of the architecture of different cognitive systems. Additionally, in the long run, they may contribute to the design of educational and rehabilitative programs for both normally and abnormally developing children.

ACKNOWLEDGMENTS This research has been supported by grants from National Institutes of Health, DC00128, and

DC00481. We are grateful to our many collaborators on the several studies summarized here, and to Linda Heidenreich for manuscript preparation. We thank Jeff Goodhill for his careful reading of this manuscript.

REFERENCES

- ARMSTRONG, B., T. MITCHELL, S. A. HILLYARD, and H. J. NEVILLE, 1995. Effects of auditory deprivation on color and motion processing: An ERP study. Ph.D. diss., University of California.
- ATKINSON, J., J. KING, O. BRADDICK, L. NOKES, S. ANKER, and F. BRADDICK, 1997. A specific deficit of dorsal stream function in Williams' syndrome. *NeuroReport* 8:1919–1922.
- BAIZER, J. S., L. G. UNGERLEIDER, and R. DESIMONE, 1991. Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *J. Neurosci.* 11:168–190.
- BLAKEMORE, C., L. J. GAREY, and F. VITAL-DURAND, 1978. The physiological effects of monocular deprivation and their reversal in the monkey's visual cortex. *Physiol. (London)* 283:223–262.
- BOWERING, E. R., D. MAURER, T. L. LEWIS, and H. P. BRENT, 1997. Constriction of the visual field of children after early visual deprivation. *J. Pediatr. Ophthalmol. Strabismus* 34:347–356.
- CHALUPA, L., and B. DREHER, 1991. High precision systems require high precision "blueprints": A new view regarding the formation of connections in the mammalian visual system. *J. Cogn. Science* 3:209–219.
- CHUGANI, H. T., R.-A. MÜLLER, and D. C. CHUGANI, 1996. Functional brain reorganization in children. *Brain Dev.* 18: 347–356.
- COHEN, L. G., P. CELNIK, A. PASCUAL-LEONE, B. CORWELL, L. FAIZ, J. DAMBROSIA, M. HONDA, N. SADATO, C. GERLOFF, M. D. CATALA, and M. HALLETT, 1997. Functional relevance of cross-modal plasticity in blind humans. *Nature* 389:180–183.
- CURTISS, S., 1989. The independence and task-specificity of language. In *Interaction in Human Development*, M. Bornstein and J. Bruner, eds. Hillsdale, N.J.: Erlbaum, pp. 105–137.
- CYNADER, M., and D. MITCHELL, 1980. Prolonged sensitivity to monocular deprivation in dark reared cats. *J. Neurophysiol.* 43:1026–1040.
- DEHAENE, S., E. DUPOUX, J. MEHLER, L. COHEN, D. PERANI, P.-F. VAN DE MOORTELE, S. LEHÉRICI, and D. LE BIHAN, 1997. Anatomical variability in the cortical representation of first and second languages. *NeuroReport* 17:3809–3815.
- DEHAY, C., J. BULLIER, and H. KENNEDY, 1984. Transient projections from the fronto-parietal and temporal cortex to areas 17, 18, and 19 in the kitten. *Exp. Brain Res.* 57:208–212.
- EDEN, G. F., J. W. VANMETER, J. M. RUMSEY, J. M. MAISOG, R. P. WOODS, and T. A. ZEFFIRO, 1996. Abnormal processing of visual motion in dyslexia revealed by functional brain imaging. *Nature* 382:66–69.
- FROST, D. O., 1984. Axonal growth and target selection during development: Retinal projections to the ventrobasal complex and other "nonvisual" structures in neonatal Syrian hamsters. *J. Comp. Neurol.* 230:576–592.
- GILBERT, C. D., 1995. Dynamic properties of adult visual cortex. In *The Cognitive Neurosciences*, M. S. Gazzaniga, ed. Cambridge, Mass.: MIT Press, pp. 73–89.

- HARWERTH, R., E. SMITH, G. DUNCAN, M. CRAWFORD, and G. VON NOORDEN, 1986. Multiple sensitive periods in the development of the primate visual system. *Science* 232:235-238.
- HICKEY, T. L., 1977. Postnatal development of the human lateral geniculate nucleus: Relationship to a critical period for the visual system. *Science* 198:836-838.
- HORTON, J. C., and D. R. HOCKING, 1997. Timing of the critical period for plasticity of ocular dominance columns in macaque striate cortex. *J. Neurosci.* 17:3684-3709.
- HUBEL, D. H., and T. N. WIESEL, 1977. Functional architecture of macaque monkey visual cortex. *Proc. R. Soc. Lond.* 198:1-59.
- HUTTENLOCHER, P. R., 1994. Synaptogenesis, synapse elimination, and neural plasticity in human cerebral cortex. In *Threats to Optimal Development: Integrating Biological, Psychological, and Social Risk Factors*, Vol. 27, C. A. Nelson, ed. Hillsdale, N.J.: Erlbaum, pp. 35-54.
- HUTTENLOCHER, P. R., and A. S. DABHOLKAR, 1997. Regional differences in synaptogenesis in human cerebral cortex. *J. Comp. Neurol.* 387:167-178.
- INNOCENTI, G., and S. CLARKE, 1984. Bilateral transitory projection to visual areas from auditory cortex in kittens. *Dev. Brain Res.* 14:143-148.
- KAAS, J. H., 1995. The reorganization of sensory and motor maps in adult mammals. In *The Cognitive Neurosciences*, M. S. Gazzaniga, ed. Cambridge, Mass.: MIT Press, pp. 51-71.
- KIM, K. H. S., N. R. RELKIN, K.-M. LEE, and J. HIRSCH, 1997. Distinct cortical areas associated with native and second languages. *Nature* 388:171-174.
- KLIMA, E. S., and U. BELLUGI, 1979. *The Signs of Language*. Cambridge, Mass.: Harvard University Press.
- LACHICA, E. A., and V. A. CASAGRANDE, 1988. Development of primate retinogeniculate axon arbors. *Vis. Neurosci.* 1:103-123.
- LIVINGSTONE, M., and D. HUBEL, 1988. Segregation of form, color, movement and depth: Anatomy, physiology, and perception. *Science* 240:740-749.
- LOVEGROVE, W., R. GARZIA, and S. NICHOLSON, 1990. Experimental evidence for a transient system deficit in specific reading disability. *J. Amer. Optom. Assoc.* 61:137-146.
- MARLER, P., 1970. A comparative approach to vocal learning: Song development in white-crowned sparrows. *J. Comp. Physiol. Psych. Monograph* 71:1-25.
- MAURER, D., and T. L. LEWIS, 1998. Overt orienting toward peripheral stimuli: Normal development and underlying mechanisms. In *Cognitive Neuroscience of Attention: A Developmental Perspective*, J. E. Richards, ed. Hillsdale, N.J.: Erlbaum, pp. 51-102.
- MERIGAN, W., and J. MAUNSELL, 1993. How parallel are the primate visual pathways? *Annu. Rev. Neurosci.* 16:369-402.
- MERZENICH, M., G. RECANZONE, W. JENKINS, T. ALLARD, and R. NUDO, 1988. Cortical representational plasticity. In *Neurobiology of Neocortex*, P. Rakic and W. Singer, eds. Chichester, U.K.: John Wiley & Sons, pp. 41-67.
- MILLS, D. L., S. A. COFFEY-CORINA, and H. J. NEVILLE, 1993. Language acquisition and cerebral specialization in 20-month-old infants. *J. Cogn. Neurosci.* 5:317-334.
- MILLS, D. L., S. A. COFFEY-CORINA, and H. J. NEVILLE, 1997. Language comprehension and cerebral specialization from 13 to 20 months. *Dev. Neuropsychology* 13:397-445.
- MIOCHE, L., and M. PERENIN, 1986. Central and peripheral residual vision in humans with bilateral deprivation amblyopia. *Exp. Brain Res.* 62:259-272.
- MITCHELL, D., 1981. Sensitive periods in visual development. In *Development of Perception*, R. Aslin, J. Alberts, and M. Petersen, eds. New York: Academic Press, pp. 3-43.
- NEVILLE, H. J., 1995. Developmental specificity in neurocognitive development in humans. In *The Cognitive Neurosciences*, M. Gazzaniga, ed. Cambridge, Mass.: MIT Press, pp. 219-231.
- NEVILLE, H. J., and D. BAVELIER, 1998. Variability of developmental plasticity within sensory and language systems: Behavioral, ERP and fMRI studies. *Proceedings of the Conference on Advancing Research on Developmental Plasticity: Integrating the Behavioral Science and the Neuroscience of Mental Health*. Washington, D.C.: U.S. Government Printing Office, pp. 174-184.
- NEVILLE, H. J., D. BAVELIER, D. CORINA, J. RAUSCHECKER, A. KARNI, A. LALWANI, A. BRAUN, V. CLARK, P. JEZZARD, and R. TURNER, 1998. Cerebral organization for language in deaf and hearing subjects: Biological constraints and effects of experience. *Proc. Natl. Acad. Sci. U.S.A.* 95:922-929.
- NEVILLE, H. J., S. A. COFFEY, D. S. LAWSON, A. FISCHER, K. EMMOREY, and U. BELLUGI, 1997. Neural systems mediating American Sign Language: Effects of sensory experience and age of acquisition. *Brain Lang.* 57:285-308.
- NEVILLE, H. J., and D. LAWSON, 1987a. Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. I. Normal hearing adults. *Brain Res.* 405:253-267.
- NEVILLE, H. J., and D. LAWSON, 1987b. Attention to central and peripheral visual space in a movement detection task: An event-related and behavioral study. II. Congenitally deaf adults. *Brain Res.* 405:268-283.
- NEVILLE, H. J., and D. LAWSON, 1987c. Attention to central and peripheral visual space in a movement detection task. III. Separate effects of auditory deprivation and acquisition of a visual language. *Brain Res.* 405:284-294.
- NEVILLE, H. J., and D. MILLS, 1997. Epigenesis of language. *Mental Retardation Dev. Disabilities Res. Rev.* 3:282-292.
- NEVILLE, H. J., D. MILLS, and D. LAWSON, 1992. Fractionating language: Different neural subsystems with different sensitive periods. *Cerebral Cortex* 2:244-258.
- NEVILLE, H. J., J. NICOL, A. BARSS, K. FORSTER, and M. GARRETT, 1991. Syntactically based sentence processing classes: Evidence from event-related brain potentials. *J. Cogn. Neurosci.* 3:155-170.
- NEVILLE, H. J., A. SCHMIDT, and M. KUTAS, 1983. Altered visual evoked potentials in congenitally deaf adults. *Brain Res.* 266:127-132.
- NOBRE, A., and G. MCCARTHY, 1994. Language-related ERPs: Scalp distributions and modulation by word type and semantic priming. *J. Cogn. Neurosci.* 6:233-255.
- OSTERHOUT, L., J. McLAUGHLIN, and M. BERSICK, 1997. Event-related brain potentials and human language. *Trends Cogn. Sci.* 1:203-209.
- PACKER, O., A. HENDRICKSON, and A. CURCIO, 1990. Developmental redistribution of photoreceptors across the *Macaca nemestrina* (pigtail macaque) retina. *J. Comp. Neurol.* 298:472-493.
- PERANI, D., S. DEHAENE, F. GRASSI, L. COHEN, S. F. CAPPAS, E. DUPOUX, F. FAZIO, and J. MEHLER, 1996. Brain processing of native and foreign languages. *NeuroReport* 7:2439-2444.
- PONTON, C. W., M. DON, J. J. EGGERMONT, M. D. WARING, B. KWONG, and A. MASUDA, 1996. Auditory system plasticity in children after long periods of complete deafness. *NeuroReport* 8:61-65.

- RAKIC, P., 1976. Prenatal genesis of connections subserving ocular dominance in the rhesus monkey. *Nature* 261:467-471.
- RAKIC, P., J. BOURGEOIS, M. ECKENHOFF, N. ZECEVIC, and P. GOLDMAN-RAKIC, 1986. Concurrent overproduction of synapses in diverse regions of the primate cerebral cortex. *Science* 232:232-235.
- RAUSCHECKER, J., and U. KNIEPERT, 1993. Auditory localization behaviour in visually deprived cats. *Eur. J. Neurosci.* 6:149-160.
- RICE, C., S. FEINSTEIN, and R. SCHUSTERMAN, 1965. Echo-detection ability of the blind: Size and distance factors. *J. Exp. Psychol.* 70:246-251.
- RÖDER, B., F. RÖSLER, and E. HENNIGHAUSEN, 1997. Different cortical activation patterns in blind and sighted humans during encoding and transformation of haptic images. *Psychophysiology* 34:292-307.
- RÖDER, B., F. RÖSLER, E. HENNIGHAUSEN, and F. NÄCKER, 1996. Event-related potentials during auditory and somatosensory discrimination in sighted and blind human subjects. *Cogn. Brain Res.* 4:77-93.
- RÖDER, B., W. TEDER-SALEJARVI, A. STERR, F. RÖSLER, S. A. HILLYARD, and H. J. NEVILLE, 1997. Auditory-spatial tuning in sighted and blind adults: Behavioral and electrophysiological evidence. *Soc. Neurosci.* 23:1590.
- SADATO, N., A. PASCUAL-LEONE, J. GRAFMAN, V. IBANEZ, M.-P. DEIBER, G. DOLD, and M. HALLET, 1996. Activation of the primary visual cortex by braille reading in blind subjects. *Nature* 380:526-528.
- SAWATARI, A., and E. M. CALLAWAY, 1996. Convergence of magnocellular and parvocellular pathways in layer 4B of macaque primary visual cortex. *Nature* 380:442-446.
- SERENO, M. I., A. M. DALE, J. B. REPPAS, K. K. KWONG, J. W. BELLIVEAU, T. J. BRADY, B. R. ROSEN, and R. G. TOOTELL, 1995. Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* 268:889-893.
- SHANKLE, W. R., R. A. KIMBALL, B. H. LANDING, and J. HARA, 1998a. Developmental patterns in the cytoarchitecture of the human cerebral cortex from birth to 6 years examined by correspondence analysis. *Proc. Natl. Acad. Sci. U.S.A.* 95:4023-4028.
- SHANKLE, W. R., B. H. LANDING, M. S. RAFIL, A. SCHIANO, J. M. CHEN, and J. HARA, 1998b. Evidence for a postnatal doubling of neuron number in the developing human cerebral cortex between 15 months and 6 years. *J. Theor. Biol.* 191:115-140.
- SHERMAN, S., 1985. Development of retinal projections to the cat's lateral geniculate nucleus. *TINS* 8:350-355.
- SHERMAN, S., and P. SPEAR, 1982. Organization of visual pathways in normal and visually deprived cats. *Psychol. Rev.* 62:738-855.
- STONER, G. B., and T. D. ALBRIGHT, 1993. Image segmentation cues in motion processing: Implications for modularity in vision. *J. Cogn. Neurosci.* 5:129-149.
- SUR, M., S. PALLAS, and A. ROE, 1990. Cross-modal plasticity in cortical development: Differentiation and specification of sensory neocortex. *TINS* 13:227-233.
- TOMANN, A., T. MITCHELL, H. J. NEVILLE, D. CORINA, G. LIU, and D. BAVELIER, 1998. Cortical reorganization for motion processing in congenitally deaf subjects. *Cogn. Neurosci. Soc.* 5:14.
- TOOTELL, R. B., J. B. REPPAS, K. K. KWONG, R. MALACH, R. T. BORN, T. J. BRADY, B. R. ROSEN, and J. W. BELLIVEAU, 1995. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* 15:3215-3230.
- UHL, F., P. FRANZEN, G. LINDINGER, W. LANG, and L. DEECKE, 1991. On the functionality of the visually deprived occipital cortex in early blind persons. *Neurosci. Lett.* 124:256-259.
- UHL, F., T. KRETSCHMER, G. LINDINGER, G. GOLDENBERG, W. LANG, W. ODER, and L. DEECKE, 1994. Tactile mental imagery in sighted persons and in patients suffering from peripheral blindness early in life. *Electroencephalogr. Clin. Neurophysiol.* 91:249-255.
- UNGERLEIDER, L. G., and M. MISHKIN, 1982. Two cortical visual systems. In *Analysis of Visual Behavior*, D. J. Ingle, M. A. Goodale, and R. J. Mansfield, eds. Cambridge, Mass.: MIT Press, pp. 549-586.
- VAN DRIEL, D., J. M. PROVIS, and F. A. BILLSON, 1990. Early differentiation of ganglion, amacrine, bipolar, and Muller cells in the developing fovea of human retina. *J. Comp. Neurol.* 291:203-219.
- VERAART, C., A. DEVOLDER, M. WANET-DEFALQUE, A. BOL, C. MICHEL, and A. GOFFINET, 1990. Glucose utilization in human visual cortex is abnormally elevated in blindness of early onset but decreased in blindness of late onset. *Brain Res.* 510:115-121.
- WANET-DEFALQUE, M., C. VERAART, A. DEVOLDER, R. METZ, C. MICHEL, G. DOOMS, and A. GOFFINET, 1988. High metabolic activity in the visual cortex of early blind human subjects. *Brain Res.* 446:369-373.
- WEBER-FOX, C., and H. J. NEVILLE, 1996. Maturation constraints on functional specializations for language processing: ERP and behavioral evidence in bilingual speakers. *J. Cogn. Neurosci.* 8:231-256.