Processes of Change in Brain and Cognitive Development

Attention and Performance XXI

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This book is based on the papers presented at the Twenty-First International Symposium on Attention and Performance held at Winter Park, Colorado, July 26–Aug 1, 2004.

OXFORD
UNIVERSITY PRESS

Chapter 13

Different profiles of plasticity within human cognition

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Abstract

Behavioral, event related potentials (ERP), and magnetic resonance imaging (MRI) studies of the development and plasticity of visual processing, auditory processing, attention, and language are reviewed. The results show that within each domain of processing there is considerable variability in the degree to which, and the time periods when, different subsystems are modifiable by experience. Some subsystems appear highly constrained and are not different even when experience is very different. Others are dependent on, and modified by, experience but only during specific time periods in human development. Still other subsystems appear to be changeable throughout life. Taken together these data raise testable hypotheses about the mechanisms of neuroplasticity.

13.1 Introduction

One of the questions that has occupied the minds of parents, educators, and philosophers for millennia, is at the heart of the research I describe here: the nature of, and the interactions between, biological constraints and the role of experience (i.e. input from the environment) in human cognitive and neural development. Although this issue has long been central in philosophical and societal debate, it has only been systematically researched over the past 40 years. It began, of course, with the work of Hubel and Weisel and their followers, who reported marked effects of visual experience on the development of visual cortex and related functions (Wiesel and Hubel 1965). Until recently, most of this research had been performed with non-human animals and was concerned with sensory development. With the advent of non-invasive methods for imaging the human brain, we can now more directly seek answers to the following questions about the human mind/brain: to what extent do different brain systems possess intrinsic constraints that make them capable of

processing some but not other types of information? What is the role of inputs from the environment in specifying the functional properties of the brain regions they contact?

These are fundamental questions about who we are and where we come from. On a practical level, answers to these questions can contribute information important to the design of educational and rehabilitative programs in that they will help us identify the functional brain systems that are most modifiable and the time periods when they are most modifiable.

Over the past several years, we have approached these questions in two ways. In the first, we have compared cerebral organization in normally hearing, seeing, monolingual, speaking adults with that observed in individuals who have had altered sensory and/or language experience. This latter group includes deaf and blind adults, bilinguals who learned English at different ages, and those who have learned a visual/manual language. The second approach has been to compare brain organization in children of different ages and stages of cognitive development, as well as before and after various intervention programs. In these studies we have used both ERPs and MRI methods. We have studied the development of perceptual/attentional systems, as well as the development of the language systems of the brain.

In this chapter, I first review the structural development of the human brain, relevant literatures on sensory plasticity, as well as our newer studies of sensory plasticity and development. Second, I review literature relevant to the plasticity and development of the language systems, as well as our newer studies along these lines.

13.2 Structural development of the human brain

The structural development of the human brain displays a protracted timecourse of postnatal development that in some regions does not reach maturity until the third decade of life. There is great variability in the rate of maturation of different neural systems and subsystems, as indexed by the extent of dendritic branching, number of dendritic spines, neuronal size and density, number and type of synapses, pharmacological composition, grey to white matter ratios, and cortical volumes (Chugani et al. 1987; Huttenlocher and Dabholkar 1997; Neville 1998). Following this protracted development, the mature human brain is a complex mosaic of systems and subsystems that display considerable specificity in their functional properties. A burgeoning literature has identified several molecular and genetic factors important in specifying aspects of the initial anatomy and physiology of developing brain systems in animals (Kahn and Krubitzer 2002; Krubitzer and Huffman 2000; Silver et al. 2001; Taha and Stryker 2002). The overarching goals of the research summarized in this chapter are to characterize both biological constraints, and the degree to which, and the time periods during which, the functional specializations of different neural systems are dependent on, and modifiable by, experience in human development.

13.3 Intra- and intermodal plasticity

During the past 30 years, research with animals has documented marked and specific effects of both sensory deprivation and training on the organization of cortical areas that represent a particular sensory system and on the development of remaining sensory modalities (Frost et al. 2000; Metin and Frost 1989; Roe et al. 1992; Sur and Garraghty 1986; von Melchner et al. 2000). These studies have shown that some neural systems and associated behavioral capabilities are affected by such experience only during specific time periods (sensitive periods) and that different systems have different sensitive periods. For example within the visual system, the development of acuity, orientation preferences, ocular dominance columns, stereopsis, and photoptic and scotopic vision display different sensitive periods (Harwerth et al. 1986; Horton and Hocking 1997; Hubel and Wiesel 1977; Mitchell 1990). This variability in the timing of experience-dependent modifiability likely arises in part from subsystem differences in rate of maturation, extent and timing of redundant connectivity and presence of chemicals and receptors known to be important in plasticity. By contrast, some neural systems appear not to be constrained by sensitive periods. For example, remapping of the representation of the visual fields following retinal lesions can occur throughout life (Kaas et al. 1990), as can remapping of the primary cortical representation of the digits following amputation or training (Merzenich and Jenkins 1993).

Recent studies support the view that in humans, as in other animals, there is considerable variability in experience-dependent plasticity. For example if cataracts are not removed by 5 months of age, visual acuity never reaches normal values, and if convergent input to the two eyes is not achieved by 11 months of age, stereopsis is not acquired (Maurer et al. 1999; Tychsen 2001). In addition, lack of patterned visual input during the first 2 to 6 months of age results in permanent deficits in configural but not featural aspects of face processing (Le Grand et al. 2001), and visual deprivation occurring as late as 6 years of age leads to deficits in the ability to orient to peripheral visual information (Kovacs et al. 2000). In contrast, other systems appear not to show sensitive period effects in humans: for example amputation in adults results in reorganization of cortical areas that formerly represented the lost limb (Elbert et al. 1994; Ramachandran et al. 1992).

13.4 Plasticity within the visual system after auditory deprivation

13.4.1 Motion and color

Anatomical, physiological, and psychophysical evidence from several lines of investigation has defined the distinction between the dorsal visual pathway, projecting from V1 to parietal cortex, that includes structures important for the processing of spatial location and motion, and the ventral visual pathway, projecting from V1 to anterior

inferior temporal cortices, that includes systems important for processing color and form information (Tootell *et al.* 1995; Ungerleider and Mishkin 1982). Further evidence confirmed that the central visual field is largely represented along the ventral pathway while the peripheral visual fields are largely represented along the dorsal pathway (Baizer *et al.* 1991). Consistent with this, in several early studies we observed that sensory and attentional processing of visual information presented to the central and peripheral visual fields elicits activity in different neural systems in normally hearing adults. Furthermore, we observed that congenital auditory deprivation – but not the acquisition of American Sign Language (ASL) – results in enhanced detection of motion and enhanced ERPs in the peripheral (but not the central) visual fields (Neville *et al.* 1983; Neville and Lawson 1987a, 1987b, 1987c; Neville 1995). These results suggested the hypothesis that the dorsal visual pathway might be more modified following auditory deprivation than the ventral pathway. To test this, we used stimuli designed to selectively activate either the parvocellular neurons that project strongly (but not solely, see, Sawatari and Callaway 1996; Stoner and Albright 1993) to the ventral pathway or the magnocellular system that projects strongly to the dorsal pathway. The parvo system is highly responsive to color information and to stimuli of high spatial frequency, while the magno system is very responsive to motion and to stimuli of low spatial frequency and low contrast (Livingstone and Hubel 1988; Merigan and Maunsell 1993).

We tested normal hearing and congenitally deaf participants. Peripheral stimuli were presented 8° from the central (foveal) stimulus in the upper and lower left and right visual fields. The parvo stimuli were isoluminant blue and green high spatial frequency gratings (adjusted for the cortical magnification factor) continuously visible at all locations. The eliciting stimulus was a color change: randomly at one location, the blue bars changed to red for 100 ms. The magno stimuli consisted of low spatial frequency gratings of light and dark gray bars with a low luminance contrast. The eliciting stimulus consisted of the bars at one location (random) moving transversely to the right for 100 ms. Research participants fixated centrally and monitored all locations for the rare occurrence of a black square (Armstrong *et al.* 2002).

In normal hearing adults the color and motion stimuli elicited ERPs that differed in their componentry, latencies, and distributions, and were consistent with the hypothesis that these stimuli activated distinct neural systems. An early positivity (100 ms) focal to medial occipital regions was largest in response to motion, and a later, lateral (130 ms) positivity was larger in response to color changes. In addition, the latency of the negativity around 170 ms (N170) was faster to motion stimuli. The earliest responses (P100, P130) were similar in deaf and hearing participants, suggesting that processing within early visual cortical areas may be unaffected by auditory deprivation. The N170 component was similar in response to color changes in deaf and hearing participants, but in response to motion it was significantly larger and was distributed more anteriorly in deaf than hearing participants (Fig. 13.1). These results
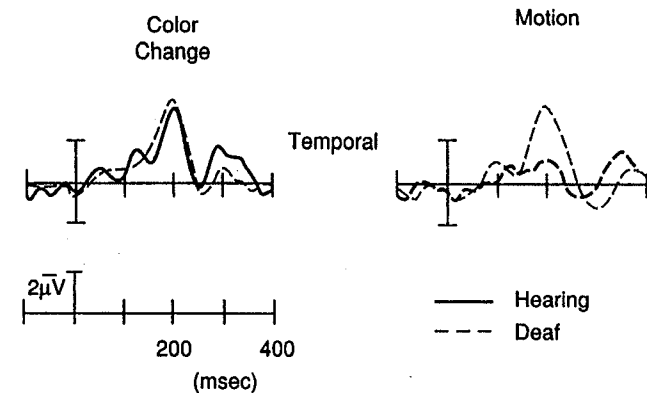
Fig. 13.1 ERPs to color and motion in normally hearing and congenitally deaf adults.

were more pronounced for peripheral than central motion. These results are consistent with the hypothesis that early auditory deprivation has more pronounced effects on the functions of the dorsal than the ventral visual pathway.

13.4.2 Motion processing

Too more precisely identify the visual areas that might underlie the enhanced behavioral and ERP responses to motion in deaf participants we employed the functional magnetic imaging (fMRI) technique (details in Bavelier *et al.* 2000). In particular, we tested the hypothesis that the middle temporal areas (MT/MST), shown in previous studies to be responsive to motion and attention to motion, displays enhanced activation in deaf as compared to hearing individuals. Participants included hearing and congenitally, genetically deaf individuals who viewed alternating blocks of static dots and flow fields of moving dots. Motion flow fields strongly recruit the motion pathway, including the motion-selective area MT/MST (O'Craven *et al.* 1997; Tootell and Taylor 1995). On separate runs, participants attended the center or the periphery (6–8°) of the display to detect luminance changes.

MT/MST was identified individually for each participant and the data were analyzed for each participant by computing the temporal correlation between the magnetic resonance (MR) signal and a reference function for each voxel. Analyses of the extent of activation in MT/MST revealed that whereas MT/MST recruitment was comparable across populations when the center of the visual field was monitored, deaf individuals displayed greater MT/MST activation than hearing participants when the peripheral visual field was monitored. This finding indicates a specific modulation of attention to peripheral moving stimuli in the deaf and suggests that changes in MT may have contributed to the behavioral and ERP effects described in our previous research (Neville and Lawson 1987b).

To further characterize the altered MT activation in the deaf, we used structural equation modeling to estimate the strength of cortical connections between early visual areas (V1/V2), area MT/MST, and part of the posterior parietal cortex (PPC) (Beauchamp and DeYoe 1996; Buchel and Friston 1997; McIntosh and Gonzalez-Lima 1994). During attention to the center the connectivity was comparable across groups but during the attend-periphery condition the effective connectivity between MT/MST and PPC was increased in the deaf as compared with the hearing participants. This finding suggests that the enhanced responsiveness to peripheral motion in deaf individuals may be specifically linked to attention.

13.4.3 Motion velocity

In this study we further characterized the effects of auditory deprivation on several motion sensitive areas and separated them from the effects of the acquisition of ASL (Bavelier et al. 2001). Congenitally deaf and hearing native signers and normally hearing controls attended either the center or periphery of a moving flow field to detect a transient acceleration of the dots. Cortical areas V1/V2, MT/MST, V3A, PPC, and posterior superior temporal sulcus (pSTS) were delineated separately for each individual on the basis of functional and anatomical criteria. We observed marked and specific differences in the recruitment of motion related areas as a function of sensory and language experience. Both of the hearing populations displayed better behavioral performance and greater recruitment of MT/MST under central than peripheral attention, whereas the opposite pattern was observed in deaf signers, indicating enhanced peripheral attention following early deafness per se. In addition, deaf signers, but neither of the hearing populations, displayed an overall increase in the activation of the PPC, supporting the view that parietal functions are significantly modified after early auditory deprivation. Finally, only in deaf signers did attention to motion velocity result in enhanced recruitment of the pSTS, establishing for the first time functionally specific compensatory plasticity in this polymodal area following altered sensory experience. These results add further support to the proposal that experience-dependent plasticity in humans can be highly specific and is likely constrained both by features of the biological substrates involved and by functionally driven processes.

In these studies, as in every other study mapping the visual field and visual attention in humans, the stimuli did not extend past 20° eccentricity, which is considered the beginning of the periphery. Recently (Scott et al. 2003), we have employed fMRI to map cortical areas sensitive to visual stimuli presented from the center of the visual field to the far periphery (2–80° eccentricity) (Scott et al. 2003). Mapping was performed along a single radial direction in four visual field quadrants, in each of four adult participants (Fig. 13.1a). A V1 mapping was clearly identified for 16 of 16 quadrants. A V2 mapping was found for 12 of 16 quadrants, though not always to the most peripheral locations. In all participants, several other occipital-parietal areas also showed retinotopic or non-retinotopic visual activation. Some of these only contained representations of the far periphery. These maps were used to estimate cortical distance as a function of eccentricity (cortical magnification factor). The cortical magnification estimate was about 20 per cent more shallow than previous estimates using other mapping techniques in the central visual field (<20°) (Engel et al. 1997). Our retinotopic mapping was performed with focused attention at the stimulus location. However, we also repeated a portion of the experiments with attention focused at the fixation point or with two or four simultaneously attended stimuli (always in different visual field quadrants). In each of these cases, the magnitude of activity was decreased or absent for more eccentric locations (>20°). As the stimulation was identical across these experiments, this result suggests that the cortical representation of space was modulated with attention and, further, that this effect increased with increasing eccentricity. Indeed this modulation with attention could have altered the cortical magnification estimate with respect to previous mapping studies that have not manipulated focused spatial attention. In ongoing research we are explicitly testing this hypothesis. In addition, we are testing the hypothesis that the effects of attention, and the extent of plastic changes in the deaf, increase with increasing eccentricity.

13.5 Plasticity and vulnerability

We are also conducting studies to assess the hypothesis that the same subsystems that display the greatest plasticity and are enhanced in deaf individuals are more vulnerable in development and will display the greatest deficits in developmental disorders, including dyslexia. A considerable body of research has reported selective deficits among at least some individuals with dyslexia in functions mediated by the magnocellular, but not parvocellular, visual pathway (Cornelissen et al. 1995; Everatt et al. 1999; Hansen et al. 2001; Lovegrove et al. 1986; Sperling et al. 2003; Talcott et al. 1998, 2000). Individuals with dyslexia also show reduced (Demb et al. 1998) or even non-significant (Eden 1996) activations in motion-sensitive areas MT/MST when processing motion stimuli, and evidence from post mortem autopsies reveal abnormalities in the magnocellular, but not parvocelluar, layers of the lateral geniculate nucleus (LGN) of adults with dyslexia (Livingstone et al. 1991).

This pattern of results has been taken to support the hypothesis that the deficits observed in visual M-pathway functions are reflective of a more general deficit in magnocellular pathways throughout the brain, including those in the medial geniculate nucleus that subserve auditory processing (Stein and Talcott 1999). An impairment in fast-processing streams could result in poor temporal integration of stimuli from the two modalities during reading, which requires both visuo-orthographic and auditory-phonological representations of letters (Breznitz and Maya 2003). However,

previous research on M- versus P-pathway visual deficits has been criticized on the grounds that the tasks used to assess M-pathway function are typically more attentionally and cognitively demanding than those used to assess P-pathway function (Newport et al. 2002). It remains unclear whether the selective M-pathway deficits observed could be explained by attentional differences in individuals with dyslexia. Preliminary data from our laboratory suggests that the visual deficit in adults with dyslexia persists even for 'simple' tasks of M-pathway function. In this study, participants indicated at which point in the far periphery (∼50°) they detected a dot moving along a straight trajectory to the center of vision. Whereas deaf participants detected the moving dots significantly sooner (i.e. at greater eccentricity) than controls, participants with dyslexia detected them significantly later than controls. By contrast, both groups performed within normal limits on a detection task in the center of the visual field (Darves and Neville 2004). These data together with other lines of evidence (Atkinson et al. 1997; Bellugi et al. 2000) support the hypothesis that more modifiable systems may be more vulnerable in developmental disorders.

13.6 Development of visual pathways

As noted, many investigators have documented greater vulnerability of the dorsal pathway in developmental disorders including dyslexia (Eden 1996; Galaburda and Livingstone 1993; Lovegrove et al. 1990, Lovegrove 1993; Livingstone et al. 1991) and Williams syndrome (Atkinson et al. 1997; Bellugi et al. 2000). In recent experiments, we tested the hypothesis that the greater modifiability/vulnerability may arise in part from a longer maturational period of the dorsal system, since the available evidence (largely psychophysical) on this is currently conflicting (Dobkins and Teller 1996; Hickey 1977; Hollants-Gilhuijs et al. 1998a, 1998b; Johnson et al. 2001). We recently tested 30 children, aged 6 to 10, on the same paradigm that we used in studies of deaf and hearing adults (Armstrong et al. 2002; Mitchell and Neville in press). ERPs were recorded to the same stimuli employed in the study of ERPs to color and motion in adults described above and in Armstrong and colleagues (2002). Whereas in adults the latency of the N100 responses to the motion stimuli were significantly earlier than the N100 latencies to the color stimuli (consistent with studies of single neurons in the two pathways), all of the children displayed the opposite pattern: responses to motion were slower than those to color (Fig. 13.2). Moreover, latencies to the color changes were equivalent in the children and adults, but the children's responses to motion were slower than those of adults (Fig. 13.2).

Additional evidence for the relative immaturity of the motion responses was evident in the amplitudes: whereas the color and motion responses were of equivalent amplitude in the adults, in children the ERP amplitudes to motion were considerably smaller than were those to color. Thus these data are consistent with the hypothesis that the greater vulnerability/modifiability of the dorsal stream may be due in part to its more protracted development.
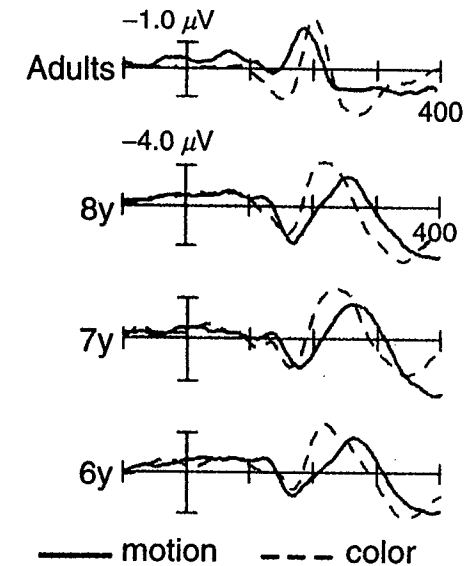

Fig. 13.2 ERPs to motion and color in adults and 6-, 7-, and 8-year-old children.

13.7 Plasticity within the auditory system after visual deprivation

To test the generality of the results from our studies of the effects of auditory deprivation, we conducted studies of the effects of visual deprivation on the development of remaining sensory systems. Although relatively little is known about the organization of the auditory system, as in the visual system there are larger (magno) cells in the medial geniculate nucleus that conduct faster than the smaller parvo cells, and recent evidence suggests that there may be dorsal and ventral processing streams with different functional specializations (Rauschecker 1995). Furthermore, animal and human studies of blindness have reported changes in parietal cortex (i.e. dorsal pathway). To determine whether parallel patterns of plasticity occur following auditory and visual deprivation we developed two auditory paradigms that are parallel to visual paradigms that we had previously employed in studies of the deaf.

In the first paradigm, participants detected infrequent pitch changes in a series of tones that were preceded by different interstimulus intervals (Röder et al. 1999a). Congenitally blind participants were faster at detecting the targets and displayed ERPs that were less refractory, that is, recovered amplitude faster than normally sighted research participants. These results are parallel to those from our study showing faster amplitude recovery of the visual ERP in deaf than hearing participants (Neville et al. 1983) and suggest that rapid auditory and visual processing may show specific enhancements following sensory deprivation.

In a second experiment, we tested the generality of our finding of a specific enhancement of the representation of the visual periphery in deaf participants. We first developed a paradigm to compare attention to central and peripheral auditory space in normal controls (Teder-Salejarvi et al. 1999a). Participants attended selectively to brief noise bursts delivered in free-field via central and peripheral arrays of speakers extending from midline to 90° right of center. In separate runs, participants selectively attended to the center or rightmost speaker to detect infrequent 'target' stimuli occurring at that location. Behavioral detection rates and concurrently recorded ERPs indicated that attentional gradients were steeper for the central than the peripheral array, indicating that attention can be more sharply focused on sound sources directly in front of the listener. In the study of congenitally blind participants, we observed that, when attending central auditory space, blind and sighted participants displayed similar localization abilities and ERP attention effects. In contrast, blind participants were superior to sighted controls at localizing sounds in peripheral auditory space and ERPs revealed sharper tuning of early spatial attention mechanisms in the blind individuals only when attending the periphery (Röder et al. 1999b). Differences in the scalp distribution of brain electrical activity between the two groups suggested a compensatory reorganization of visual areas in the blind that may contribute to the improved spatial resolution for peripheral sound sources.

13.8 Development of sustained attention

The results showing increased auditory attention in the blind suggest that auditory attention may also be a system displaying a long developmental timecourse. Behavioral studies have indicated that auditory selective attention skills develop throughout childhood at least until adolescence. Both the abilities to selectively attend to relevant stimuli and to successfully ignore irrelevant stimuli improve progressively with increasing age across childhood (Doyle 1973; Geffen and Sexton 1978; Geffen and Wale 1979; Hiscock and Kinsbourne 1980; Lane and Pearson 1982; Maccoby and Konrad 1966; Sexton and Geffen 1979; Zukier and Hagen 1978). The ability to shift attention quickly and effectively also develops across childhood, at least until adolescence (Andersson and Hugdahl 1987; Geffen and Wale 1979; Hiscock and Kinsbourne 1980; Pearson and Lane 1991). Furthermore, there is some evidence that background noise creates greater masking effects for younger children as compared to adolescents or adults (Elliott 1979).

Although behavioral studies offer evidence for the development of selective auditory attention in school-age children, there is little comparable electrophysiological evidence from children in this age range. One published study employed a typical ERP dichotic listening attention paradigm using tones and syllables with young participants (groups with mean age 8 and 14 years) (Berman and Friedman 1995). The

expected effect of attention (increased NI amplitude or Nd) was observed in all participants, with Nd amplitude increasing with age, more so for syllables than for tones. The primary effect of age appeared to be smaller negative ERPs elicited by stimuli in the unattended channel, which the authors suggested might reflect a narrowing of attentional focus or greater facility in suppressing unattended inputs with age (Berman and Friedman 1995).
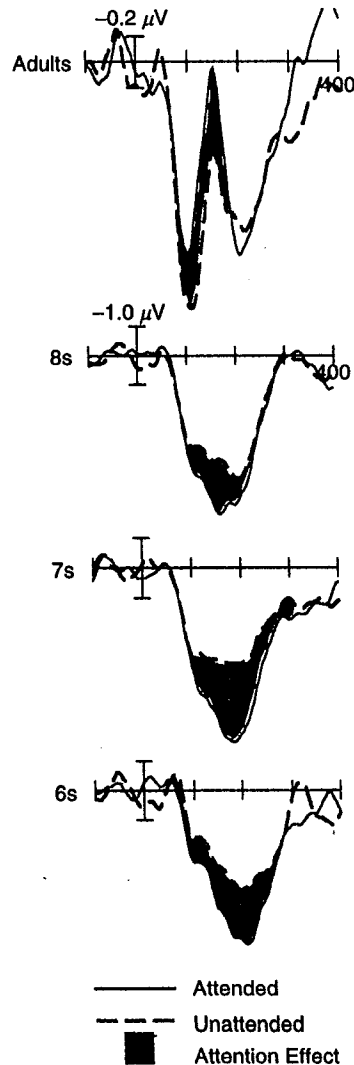
Moreover, in the selective auditory attention paradigm, the expected N100 attention effect was observed in control adolescents aged 12 to 14 (Loiselle et al. 1980). Other studies have reported similar attention effects in adolescent boys (Lovrich et al. 1983; Zambelli et al. 1977).

Recently we developed a dichotic listening task to characterize the development of sustained auditory attention across the early school age years. Our paradigm was modeled after those that we and many others have employed in adults (Hillyard et al. 1973; Röder et al. 1999b; Spezio et al. 2000; Teder-Salejarvi et al. 1999a, Teder-Salejarvi et al. 1999b; Woods et al. 1984) and was designed to be difficult enough to demand and switch focused selective attention alone, while keeping the physical stimuli, arousal levels, and task demands constant (Coch et al. in press; Woods et al. 2002a, 2002b). Two children's stories (one read by a man, one by a woman) were presented concurrently from speakers to the left and right of a central monitor. Participants were asked to attend to one story and ignore the other. Every so often the stories switched sides and a pointing cartoon character on the monitor reminded research participants to follow the attended story to the other side. Superimposed on the stories were linguistic and non-linguistic 'probe' stimuli to which ERPs were recorded: these were a 100 ms token of the syllable ba and a 100 ms 'buzz' created by scrambling 6 ms segments of the ba so that the frequency spectra and other acoustic characterizations of the two stimuli were the same. After the experiment, participants were asked questions about the attended and unattended stories.

We first tested 16 adults on this paradigm. ERPs to the attended and unattended probes elicited the classic effects of auditory attention including enhanced negativity to the probes when attention was directed toward as compared to away from them (Fig. 13.3). We then tested 24 6-year-olds, 24 7-year-olds, and 24 8-year-olds. Behaviorally, all groups performed well; however, the percent of correctly answered questions increased with age for the attended story and decreased for the unattended story. The ERPs from each age group showed clear and significant attention effects, however, these were opposite in polarity to those in the adults; that is, when attended, probes elicited greater positivity than when unattended (Fig. 13.3). However, the attention effect to the non-linguistic probes displayed an anterior bilateral distribution in all groups. The attention effect to the linguistic probes displayed a different distribution in the children and adults. These results indicate that slowly developing, non-identical neural systems mediate aspects of linguistic and non-linguistic auditory attention.

13.9 Plasticity within the language systems

It is reasonable to propose that the principles and mechanisms that govern the development of sensory systems also guide the development of neural systems important for language processing. In particular, to the extent that different subsystems within language depend on non-identical neural substrates with different developmental time courses, it is likely that they display different patterns of experience-dependent plasticity. One way this question has been investigated is to compare cerebral organization in adults who learned language at different times in development.

13.9.1 Delayed second language acquisition

Changes in several postnatal maturational processes during neural development have been implicated as potential mechanisms underlying sensitive period phenomena. Lenneberg (1967) hypothesized that maturational processes similar to those that govern sensory and motor development may also constrain capabilities for normal language acquisition. In this study, we investigated the hypothesis that maturational constraints may have different effects upon the development of the functional specializations of distinct subsystems within language (Weber-Fox and Neville 1996a). Research participants were Chinese/English bilinguals who were exposed to English at different points in development. ERPs and behavioral responses were obtained as participants read sentences that included semantic anomalies, three types of syntactic violations (phrase structure, specificity constraint, and subjacency constraint), and their controls. Accuracy in judging the grammaticality of the different types of syntactic sentences and their associated ERPs were affected by delays in second language exposure as short as 4 to 6 years. By comparison, the N400 response and the behavioral accuracy in detecting semantic anomalies were altered only in participants who were exposed to English after 11 to 13 and 16 years of age, respectively. Furthermore, the type of ERP changes concomitant with delays in exposure were qualitatively different for semantic and syntactic processing. All groups displayed a significant N400 effect in response to semantic anomalies. However, the peak latencies of the N400 elicited in bilinguals who were exposed to English between 11 and 13 and greater than 16 years occurred later, suggesting a slight slowing in processing. For syntactic processing, ERP differences associated with delays in exposure to English were observed in the morphology and distribution of components. Our findings are consistent with the view that maturational changes significantly constrain the development of neural systems relevant for language, and, in addition, that subsystems specialized for processing different aspects of language display different sensitive periods (Weber-Fox and Neville 1996b).

In similar groups of monolingual and Chinese/English bilinguals we compared responses to open- and closed-class words embedded in normal, written sentences to further explore the hypothesis that there are different effects of delays in language exposure on the processing of words that carry different amounts of semantic and grammatical information (Weber-Fox and Neville 1999). Whereas the latencies and distributions of the N350 response to open-class words were similar in all groups of research participants, the peak latency of the N280 response to closed-class words was significantly delayed in all groups exposed to English after 7 years of age. In both of

Fig. 13.3 Effects of selective auditory attention on ERPs from adults and 6-, 7-, and 8-year-old children.

these studies we were able to separately assess the contributions of age of exposure and years of experience. The results clearly show that delays in L2 acquisition have more pronounced effects on grammatical than on lexical–semantic aspects of language processing.

13.9.2 Sentence processing in American Sign Language

The study of ASL provides a rare opportunity to determine which of the language-relevant aspects of cerebral organization are independent of the modality of language production and perception and so therefore may be candidates for biological universals of language. It also provides the opportunity to isolate those modality-specific effects that are determined by the nature of language experience. In several studies we have attempted to extend to ASL our findings from studies of English that suggest that different subsystems mediate aspects of grammatical and semantic processing and that subsystems have different sensitive periods. In addition, we investigated different hypotheses that could account for why, in earlier studies (Neville et al. 1992), our deaf participants did not display evidence for specialization within the left hemisphere when processing English. It could be, as has been proposed by several investigators, that the left hemisphere is specifically specialized for the auditory encoding of language and for the visual to auditory or 'phonological' decoding that characterizes reading by hearing, but not deaf, individuals. However, if grammatical recoding is an important variable in the development of left hemisphere specialization for a language (Liberman 1974), then deaf participants should display left hemisphere specialization when processing ASL. In fact, a sizeable literature has accumulated during the past 100 years that suggests lesions to the left hemisphere impair the use of signed languages in much the same way as is the case for spoken languages (Corina 2002; Hickok et al. 1996; Poizner et al. 1987). Less is known about the contribution of the right hemisphere (RH) to sign language, as fewer right hemisphere damaged deaf patients have been studied systematically, and the results are not consistent. However, language comprehension deficits have been reported following right hemisphere damage (Corina 2002; Poizner et al. 1987; Poizner and Tallal 1987).

In one study, ERPs were recorded from deaf and hearing native signers as they viewed ASL signs that formed sentences. The results suggest that there are constraints on the organization of the neural systems that mediate formal languages and that these are independent of the modality through which language is acquired. These include different specializations of anterior and posterior cortical regions for aspects of grammatical and semantic processing and a bias for the left hemisphere to mediate aspects of mnemonic functions in language. In addition, the results suggest that the nature and timing of sensory and language experience significantly impacts the development of the language systems of the brain. Effects of early acquisition of ASL include an increased role for the right hemisphere and parietal cortex that occurs in both hearing and deaf native signers. An increased role of posterior temporal and

occipital areas occurs only in deaf native signers and thus may be attributable to auditory deprivation (Neville et al. 1997).

Because our ERP evidence for right hemisphere activation in ASL was unexpected given previous clinical studies, we began a series of fMRI studies to more precisely specify and compare the brain areas active in processing ASL and English. Effects of deafness, age of language acquisition, and bilingualism were assessed by comparing results from: (a) normally hearing, monolingual, native speakers of English; (b) congenitally, genetically deaf, native signers of ASL who learned English late and through the visual modality; and (c) normally hearing bilinguals who were native signers of ASL and speakers of English. All groups, hearing and deaf, processing their native language, English or ASL, displayed strong and repeated activation within classical language areas of the left hemisphere. Deaf native signers reading English did not display activation in these regions, suggesting that the early acquisition of a natural language is important in the expression of the strong bias for these areas to mediate language, independently of the form of the language. In addition, native signers (hearing and deaf) processing ASL (but not English) displayed extensive activation of homologous areas within the right hemisphere, indicating that the specific processing requirements of the language also, in part, determine the organization of the language systems of the brain (Bavelier et al. 1998; Neville et al. 1998). Since our publication, other groups have performed related studies and report evidence of left and right temporal lobe activation during ASL processing (Petitto et al. 2000; Soederfeldt et al. 1997).

To assess the possibility that the increased right hemisphere activation to signed as compared to written sentences might be attributable to factors including the presence of prosody in ASL (but not in written sentences), we compared activation for written and signed sentences with that for sentences spoken by a person that was both heard and viewed. Activations for spoken and written sentences were both strongly left-lateralized, in contrast to the activations for ASL sentences, which were bilateral or larger over the right hemisphere (Capek et al. 1998, 2004).

In a recent study we assessed the hypothesis that for ASL, like other natural languages, there may be a sensitive period beyond which exposure to the language is associated with deficits in acquisition and altered brain organization (Newman et al. 2002). As described above, when native learners of ASL view ASL sentences, in addition to LH activation, they show a unique pattern of extensive RH activation. In this study, we demonstrated that one of these RH regions, the angular gyrus, is active when hearing native signers process ASL, but not when late learners, who acquired ASL after puberty, do so. This suggests the existence of a sensitive period, during which, but not after, the acquisition of ASL results in the recruitment of the angular gyrus for language processing. This result has implications both for language acquisition, and more broadly for an understanding of age-related changes in neuroplasticity (Newman et al. 1998, 2002).

As noted above, studies of written and spoken language suggest that non-identical neural subsystems mediate semantic and syntactic processing. While these effects have been found for a variety of semantic and syntactic permutations in spoken languages, there is a paucity of research investigating semantic and syntactic processing in sign languages. The evidence reviewed above suggests that ASL depends upon many of the same neural systems as spoken language, but also recruits additional brain regions, primarily in the right hemisphere. In this study, we recorded ERPs from congenitally deaf native signers of ASL as they viewed semantically or syntactically appropriate and anomalous ASL sentences. As with written/spoken sentence processing, semantic violations elicited a central posterior N400 ERP response, while syntactic violations elicited an early anterior negativity followed by a broadly distributed posterior late positive shift. This pattern of results closely parallels results for spoken language and suggests modality independent universals in the language systems of the brain. However, in contrast to spoken/written language, the lateral distribution of the early negativity varied as a function of the type of syntactic agreement violation, suggesting that both biological constraints and experience shape the development of neural systems important for language.

13.9.3 Delay in first language acquisition

As noted above, many investigations of the critical or sensitive period for language have examined the effects of delays in second language acquisition on proficiency and brain organization for that language. Although effects of such delays have been reported it has been difficult to determine whether these are the result of changes in cortical maturation that limit the time periods when a language can be optimally acquired or whether they are due to interference from the first language. The deaf population provides a rare and powerful opportunity to address this issue because more than 90 per cent of deaf people are born to hearing parents who try to teach their children to speak and/or lip read. Understandably, many fail and thus the acquisition of a first language is delayed until they are exposed to ASL.[1] Behavioral studies of such individuals indicate that with increasing age of acquisition, proficiency decreases (Newport 1990; Mayberry and Eichen 1991; Mayberry 1993; Mayberry et al. 2002; Mayberry 2003), however there have not been studies of brain organization of delayed first language acquisition. We have recently studied groups of deaf individuals who acquired ASL either from birth, from 2 to 10 years or between 11 and 21 years of age (Capek et al. 2003; Capek 2004; Capek et al. in prep). We employed the ERPs paradigm described above to separately assess the effects of delayed acquisition of a first language on semantic and syntactic processing. The results clearly show that the N400 index of semantic processing displayed the same amplitude, latency and cortical

[1] While some deaf people communicate with their families using common gestures, such systems are not full languages.

distribution in all three groups of participants. However, the early anterior negativity thought to index more automatic aspects of syntax was only evident in those who acquired ASL before the age of 10 years. These results strongly indicate that interference effects from a first language are not necessary in order to observe the effects of delayed language acquisition and supports the hypothesis that there are maturational constraints that determine the optimal time period for the acquisition of a first language.

13.9.4 Language processing following visual deprivation

Individuals blind since birth provide another important opportunity to assess the effects of altered sensory and language experience on the development of language-relevant brain systems. We employed ERPs to test the hypothesis that auditory language processing occurs more rapidly in blind than sighted adults. We confirmed this hypothesis in two experiments, one of sentence processing and the other of auditory memory (Röder et al. 2000; Röder et al. 2001). In addition, we hypothesized that, in the absence of visuospatial input to the right hemisphere (which in normal development gradually becomes less responsive to auditory language (Neville and Mills 1997)), the right hemisphere may retain the capacity for processing auditory language, resulting in a more bilateral pattern of activation in blind individuals. This hypothesis was strongly confirmed, suggesting that many factors, including age of acquisition, modality of the language acquired, and the presence of other specialized brain systems operate together to determine the mature pattern of hemispheric specialization for language.

We also recently used fMRI to map language-related brain activity in congenitally blind adults (Röder et al. 2002). Participants listened to sentences, with either an easy or a more difficult syntactic structure, which were either semantically meaningful or meaningless. Results show that blind adults not only activate classical LH perisylvian language areas during speech comprehension, as did a group of sighted adults, but that they additionally display an activation in the homologous RH structures and in extrastriate and striate cortex. Both the perisylvian and occipital activity varied as a function of syntactic difficulty and semantic content. The results demonstrate that the cerebral organization of complex cognitive systems such as the language system is significantly shaped by the input from the environment.

13.9.5 Individual differences in semantic and grammatical processing

In studying the development and role of experience in the differentiation of the semantic and syntactic subsystems described above, we adapted the stimuli we have used in studies of adults for use with children. In the course of validating this new sentence set we demonstrated that it elicited effects comparable to those we have previously reported in adults and that, in addition, there were considerable individual
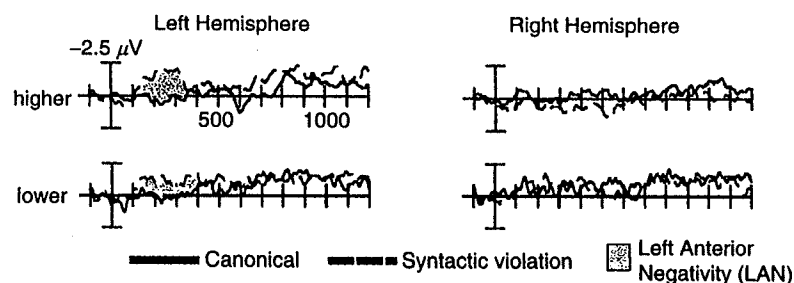
Fig. 13.4 Adult native English speakers: individuals scoring high and low on tests of grammar. ERPs to syntactically canonical and anomalous auditory sentences.

differences in the data from adult participants (Pakulak *et al.* 2002; Yamada *et al.* 2002). In follow-up studies we compared responses to these sentences in normal, monolingual adults who scored high and low on a standardized test of grammatical knowledge (Test of Adolescent and Adult Language-3, Hammil *et al.* 1994). The results clearly show the typical left-lateralized effects for closed-class words and grammatical anomalies in high scoring individuals, but significant reductions of these effects in low scoring individuals. These results were replicated in the visual and auditory modalities (Fig. 13.4).

We have also tested 30 children aged 32 to 38 months on these sentences. Whereas semantic anomalies elicited a clear N400 response with a bilateral posterior distribution similar to adults, the grammatical anomalies elicited an anterior negativity that tended to be larger over the left hemisphere (LAN). However, the onset of this effect was 200 ms later than that seen in adults. (Adamson 2000; Adamson-Harris *et al.* 2000; Fig. 13.5).

We observed considerable individual variability in these effects in the children. To assess the hypothesis that differences in language knowledge might account for this variability we compared responses from children of the same age (35 months) who scored high (84th percentile) on tests of language (Dunn and Dunn 1997; Semel *et al.* 1995) and those scoring lower (but well within normal limits – approximately 50th percentile). These analyses clearly show that the LAN effect to the grammatical anomalies is present in the high scoring children but is not reliably present in the lower scoring children (Fig. 13.6).

In ongoing studies, we are employing this paradigm in larger groups of 3-, 4- and 5-year-old children to determine when these systems are reliably present and distinct. In addition we are exploring the different factors that may determine the large individual differences in language knowledge and rate of maturation of these systems. Considerable behavioral data show that children with more talkative parents have higher language proficiencies than those with less talkative parents (Hart and Risley 1999; Huttenlocher *et al.* 1991; Huttenlocher *et al.* in press). These results can be (and have been) interpreted
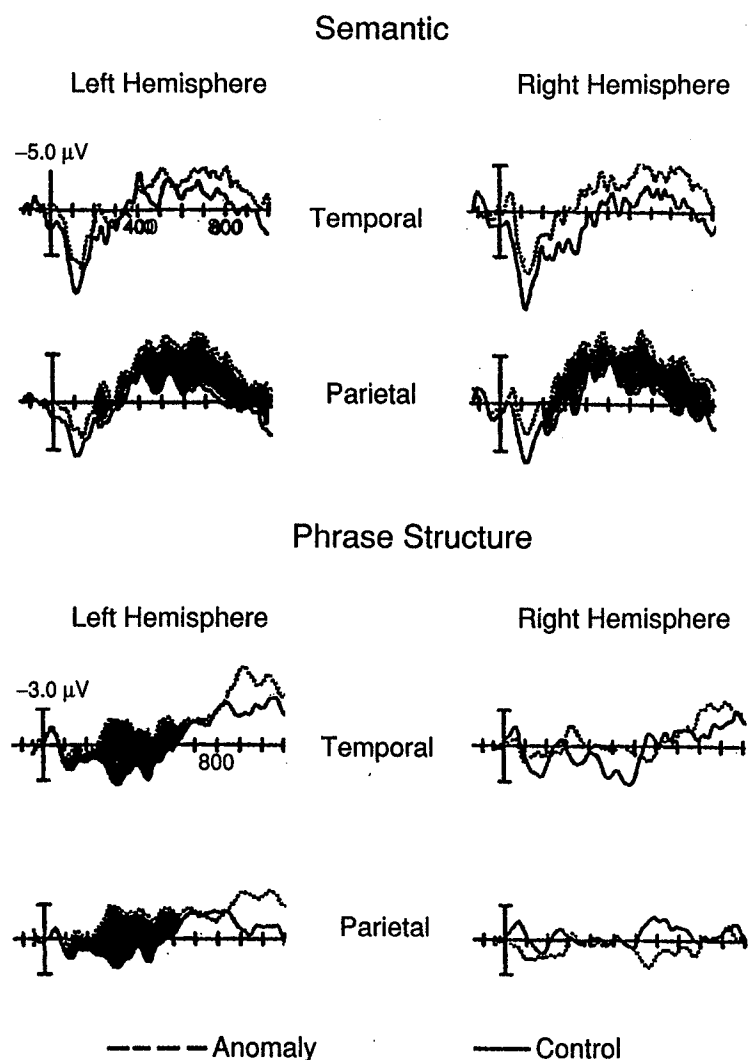
Fig. 13.5 ERPs to semantically and grammatically canonical auditory sentences in 3-year-old children.

either as showing: (a) that experience drives neural development (Hart and Risley 1999); or (b) that genetic factors shared by parents and children determine individual differences in language proficiency and brain organization (Pinker 2002). The problem of course is that children and parents share both genes and environment.

Although it is widely accepted that language acquisition depends in part on innate, intrinsic structures and in part on environmental input, few behavioral studies have
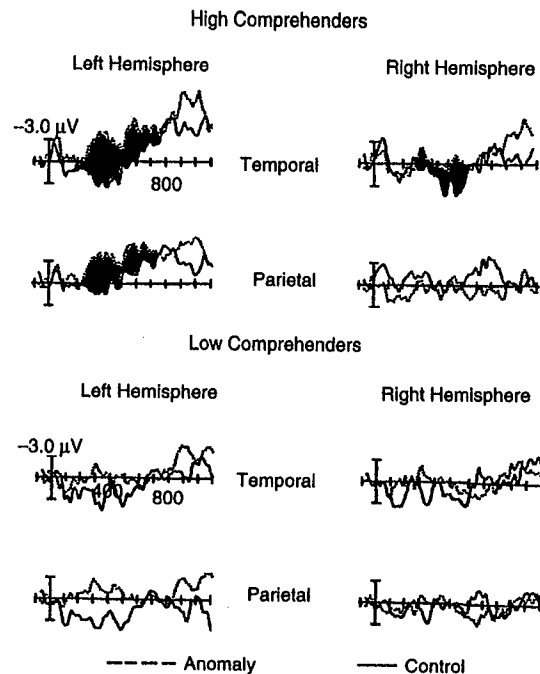
Fig. 13.6 ERPs to grammatically canonical and anomalous auditory sentences in 3-year-old children scoring high or low on tests of grammar and comprehension.

separately assessed the contribution of intrinsic and extrinsic variables to language proficiency, and none have directly assessed the effects of language input on the development of language-relevant neural systems in the developing child. Therefore, in ongoing studies, we are assessing the hypothesis that normal variation in language input from children's teachers and specific interventions drive change in these systems in normal children.

Acknowledgement

This paper is adapted from one entitled Development and Plasticity of Human Cognition to appear in Mayr *et al.* (eds), *Developing Individuality in the Human Brain: A Tribute to Mike Posner*. APA Books

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