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Profiles of Development and Plasticity in Human Neurocognition

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Abstract: ***We describe changes in neural organization and related aspects of processing after naturally occurring alterations in auditory, visual, and language experience. The results highlight the considerable differences in the degree and time periods of neuroplasticity displayed by different subsystems within vision, hearing, language, and attention. We also describe results showing the two sides of neuroplasticity, that is, the capability for enhancement and the vulnerability to deficit. Finally we describe several intervention studies in which we have targeted systems that display more neuroplasticity and show significant improvements in cognitive function and related aspects of brain organization.***

1. Introduction

Extensive research has elucidated both genetic and environmental factors that constrain and shape neuroplasticity Such research, together with noninvasive neuroimaging and genetic sequencing techniques, has guided a burgeoning literature characterizing the nature, time course, and mechanisms of neuroplasticity in humans . Electron microscopic studies of synapses and neuroimaging studies of metabolism and of gray and white matter development in the human brain reveal a generally prolonged postnatal development that nonetheless displays considerable regional variability in time course. In general, development across brain regions follows a hierarchical progression in which primary sensory areas mature before parietal, prefrontal, and association regions important for higher-order cognition .Within each region there is a pattern of prominent overproduction of synapses, dendrites, and gray matter that is subsequently pruned back to about 50% of the maximum value, which is reached at different ages in different regions. The prolonged developmental time course and considerable pruning of connections are considered major forces that permit and constrain human neuroplasticity. Recently an additional factor that appears to be important has been identified. The occurrence of polymorphisms in some genes is widespread in humans and rhesus monkeys but apparently not in other primate species. Polymorphisms provide the capability for environmental modification of the effects of gene expression (gene × environment interactions), and such effects have been observed in rhesus monkeys and humans. For several years we have employed psychophysics, electrophysiological (ERP), and magnetic resonance imaging (MRI) techniques to study the development and plasticity of the human brain. We have studied deaf and blind individuals, people who learned their first or second spoken or signed language at different ages, and children of different ages and of different cognitive capabilities. As detailed in the sections that follow, in each of the brain systems examined in this research—including those important in vision, audition, language, and attention—we observe the following characteristics:

- Different brain systems and subsystems and related sensory and cognitive abilities display different degrees and time periods ("profiles") of neuroplasticity. These may depend on the variable time periods of development and redundant connectivity displayed by different brain regions.
- Neuroplasticity within a system acts as a double-edged sword, conferring the possibility for either enhancement or deficit.
- Multiple mechanisms both support and constrain modifiability across different brain systems and subsystems. In the sections that follow, we describe our research on neuroplasticity within vision, audition, language, and attention.

2. Vision

In a number of studies we observe that some, but not all, aspects of visual function are enhanced in deaf adults. Those aspects of vision showing the greatest changes are mediated by structures along the dorsal visual pathway that have been shown to be important in the representation of the peripheral visual fields, as well as in motion processing. By contrast, aspects of processing mediated by the ventral visual pathway, including color perception and processing within the central visual field, are not altered .For example, congenitally deaf individuals have superior motion detection compared with hearing individuals for peripheral, but not central, visual stimuli. These behavioral improvements are accompanied by increases in the amplitudes of early event-related potentials (ERPs) and increased functional magnetic resonance imaging (fMRI) activation in motion-sensitive middle temporal (MT) and middle superior temporal (MST) areas of the dorsal visual pathway. In a study comparing ERPs to isoluminantcolor stimuli (designed to activate the ventral pathway) and motion stimuli (designed to activate the dorsal pathway), no differences were observed between hearing and congenitally deaf individuals in ERPs to color stimuli. In contrast, ERPs to motion were significantly larger and distributed more anteriorly in deaf than in hearing subjects. These differences were only observed for stimuli presented in the peripheral visual field . 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. A parallel literature on developmental disorders suggests that the dorsal visual pathway might also be more vulnerable to deficit in certain developmental disorders, including autism, These results are parallel and opposite to those described previously showing improved behavioral performance and increased MT/MST activation in response to motion stimuli in congenitally deaf adults. Taken together, these data suggest that the dorsal visual pathway may exhibit a greater degree of neuroplasticity than the ventral visual pathway, rendering it capable of either enhancement (as is the case following congenital deafness) or deficit (as is the case in some individuals with some developmental disorders).

3. Audition

To test whether the specificity of plasticity observed in the visual system generalizes to other sensory systems, we have conducted studies of the effects of visual deprivation on the development of the auditory system. Although less is known about the organization of the auditory system, as in the visual system there are large (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 auditory processing streams with different functional specializations. Furthermore, animal and human studies of blindness have reported changes in the parietal cortex (i.e., dorsal pathway) as a result of visual deprivation .To determine whether similar patterns of plasticity occur following auditory and visual deprivation, we developed an auditory paradigm similar to one of the visual paradigms employed in our studies of deaf adults. Participants detected infrequent pitch changes in a series of tones that were preceded by different interstimulus intervals. Congenitally blind participants were faster at detecting the target and displayed ERPs that were less refractory, that is, recovered amplitude faster than normally sighted participants. These results parallel those of our study showing faster amplitude recovery of the visual ERP in deaf than in hearing participants and suggest that rapid auditory and visual processing may show specific enhancements following sensory deprivation. Similar to the two sides of plasticity observed in the dorsal visual pathway, the refractory period for rapidly presented acoustic information, which is enhanced in the blind, shows deficits in many developmental disorders. In a study of children with specific language impairment (SLI), we observed that auditory ERPs were smaller (i.e., more refractory) than in controls at short interstimulus intervals. This finding suggests that in audition, as in vision, neural subsystems that display more neuroplasticity show both greater potential for enhancement and also greater vulnerability to deficit under other conditions.

4. Language

It is reasonable to hypothesize that the same principles that characterize neuroplasticity of sensory systems—including different profi les, degrees, and mechanisms of plasticity—also characterize language. Here, we focus on the subsystems of language examined in our studies of neuroplasticity, including those supporting semantics, syntax, and speech segmentation. Several ERP and fMRI studies have described the nonidentical neural systems that mediate semantic and syntactic processing. These neurophysiological markers of language processing show a degree of biological invariance as they are also observed when deaf and hearing native signers process American Sign Language (ASL) . While spoken and signed language processing share a number of modalityindependent neural substrates, there is also specialization based on language modality. The processing of ASL, for example, is associated with additional and/or greater recruitment of right-hemisphere structures, perhaps owing to the use of spatial location and motion in syntactic processing in ASL .In support of this hypothesis, we have recently shown that syntactic violations in ASL elicit a more bilateral anterior negativity for violations of spatial syntax, whereas a left-lateralized anterior negativity is observed for other classes of syntactic violations in ASL (Capek et al., under review).To the extent that language is made up of distinct neural subsystems, it is possible that, as in vision and audition, these subsystems show different profiles of neuroplasticity. In support of this hypothesis, behavioral studies of language proficiency in second-language learners document that phonology and syntax are particularly vulnerable following delays in second-language acquisition. Many deaf children are born to hearing parents and, because of their limited access to the spoken language that surrounds them, do not have full access to a first language until exposed to a signed language, which often occurs very late in development. Behavioral studies of deaf individuals with delayed exposure to sign language indicate that with increasing age of acquisition, proficiency in sign language decreases

5. Attention

As noted previously, many of the changes in vision, audition, and language observed in studies of neuroplasticity may depend at least in part on selective attention. The importance of selective attention for certain types of adult neuroplasticity is strongly supported by animal research. For example, when monkeys are provided with extensive exposure to auditory and tactile stimuli, experience-dependent expansions in associated auditory or somatosensory cortical areas occur, but only when attention is directed toward those stimuli in order to make behaviorally relevant discriminations (Recanzone, Jenkins, Hradek, &Merzenich, 1992; Recanzone, Schreiner, &Merzenich, 1993). Mere exposure is not enough. These data strongly suggest that attention is important in enabling neuroplasticity. Given this suggestion, as well as the central role of attention in learning more generally, we have conducted several studies on the development and neuroplasticity of attention.

6. Conclusions

The research described in this chapter has illustrated the variable degrees and time periods of neuroplasticity in the human brain and likely mechanisms whereby experience influences different subsystems within perceptual and cognitive domains. Additionally, this research has highlighted the bidirectional nature of plasticity—those aspects of neural processing and related cognitive functioning that show the greatest capability for enhancement also display the greatest susceptibility to deficits under different conditions. Researchers are entering an exciting frontier of neuroplasticity research that takes the results of basic research on the profi les and mechanisms of neuroplasticity as a point of departure in the development of training and intervention programs. Our growing

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understanding of the limits and mechanisms of plasticity contributes to a basic understanding of human brain development and function and can also inform and guide efforts to harness neuroplasticity both to optimize and to protect the malleable and vulnerable aspects of human development. acknowledgments We thank our many collaborators in the research reported here.

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