

# Profiles of Development and Plasticity in Human Neurocognition

*Courtney Stevens<sup>1</sup> and Helen Neville<sup>2</sup>*

<sup>1</sup>Willamette University

<sup>2</sup>University of Oregon

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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 timeperiods of neuroplasticity displayed by different subsystems within vision, hearing, language and attention. We also describe results showing the two sides of neuroplasticity i.e. 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.

Extensive research on animals has elucidated both genetic and environmental factors that constrain and shape neuroplasticity (Hunt et al., 2005; Garel et al., 2003; Bishop et al., 1999; Bishop, 2003). Such research together with non-invasive neuroimaging and genetic sequencing techniques have guided a burgeoning literature characterizing the nature, timecourse, and mechanisms of neuroplasticity in humans (Pascual-Leone et al., 2005; Bavelier & Neville, 2002; Movshon & Blakemore, 1974). 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 timecourse. (Chugani et al., 1987; Huttenlocher & Dabholkar, 1997; Neville, 1998; Webb et al., 2001). 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 (Giedd et al., 1999; Gogtay et al., 2004). Within each region there is a pattern of prominent overproduction of synapses, dendrites, and grey 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 timecourse and considerable pruning of connections are considered major forces that permit and constrain human neuroplasticity. Recently an additional factor has been identified which appears to be important. 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 x environment interactions) and such effects have been observed in rhesus monkeys and humans (Suomi, 2003; Suomi, 2004; Suomi, 2006; Sheese et al., 2007; Bakermans-Kranenberg et al., 2008).

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

timeperiods 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. In each section, we note different profiles of plasticity observed in the system, situations in which enhancements versus deficits are observed, and likely mechanisms contributing to these different profiles of plasticity. A final section describes our preliminary studies testing the hypothesis, raised by this basic research on human neuroplasticity, that interventions that target the most plastic, and thus potentially vulnerable, neurocognitive systems can protect and enhance children with, or at risk for, developmental deficits.

## I. 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, and 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 (Baizer et al., 1991; Bavelier et al., 2001; Corbetta et al., 1990; Livingstone & Hubel, 1988; Merigan, 1989; Merigan & Maunsell, 1990; Schiller & Malpeli, 1978; Ungerleider & Mishkin, 1982; Ungerleider & Haxby, 1994; Zeki et al., 1991). For example, congenitally deaf individuals have superior motion detection than hearing individuals for peripheral, but not central, visual stimuli (Neville et al., 1983; Neville & Lawson, 1987b; Stevens & Neville, 2006). 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 (Bavelier et al., 2000; Bavelier et al., 2001; Neville et al., 1983; Neville & Lawson, 1987b).

In a study comparing ERPs to isoluminant color 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 hearing subjects. These differences were only observed for stimuli presented in the peripheral visual field (Armstrong et al., 2002). 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, Williams, and Fragile X syndromes and reading or language impairments (Atkinson, 1992; Atkinson et al., 1997; Eden et al., 1996). For example, a number of studies indicate that at least some individuals with specific reading disorder, or dyslexia, have lower sensitivity to detecting coherent motion in random-dot kinetograms despite showing

normal thresholds for detecting coherent form in similar arrays of static line segments (Cornelissen et al., 1995; Everatt et al., 1999; Hansen et al., 2001; Talcott et al., 2000). Dyslexic individuals also show higher thresholds for detecting changes in the speed of motion flow fields (Demb et al., 1998), as well as higher critical flicker fusion thresholds for monochromatic, but not isoluminant, color stimuli when tested with a paradigm using identical task structure to assess each visual pathway (Sperling et al., 2003). In addition, there are reports that dyslexic individuals show deficits in pattern contrast sensitivity for high-contrast, low-spatial frequency gratings (Lovegrove et al., 1986). The behavioral evidence for a visual deficit in dyslexia has been corroborated by recent neuroimaging studies showing decreased (Demb et al., 1998) or even non-significant (Eden et al., 1996) activations in motion-sensitive areas MT/MST of dyslexic individuals, though no differences are observed during stationary pattern processing (Eden et al., 1996). These results are parallel and opposite to those described above 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). However, the two literatures have developed largely in parallel, and different tasks have been used to assess dorsal and ventral visual pathway function in each literature. To address this limitation, in a recent study we used the same tasks to assess visual function in both dyslexic adults and congenitally deaf adults, as well as matched controls (Stevens & Neville, 2006). We observed that whereas neither deaf nor dyslexic adults differ from matched controls on a central visual field contrast sensitivity task (Fig. 1a), on a peripheral motion detection task deaf adults show enhancements whereas dyslexic adults show deficits on the same task (Fig. 1b). These findings help bridge the two literatures and suggest that the dorsal and ventral pathways show different profiles of neuroplasticity.

A number of mechanisms may render the dorsal pathway more developmentally labile, either to enhancement or deficit, including subsystem differences in rate of maturation, extent and timing of redundant connectivity, and presence of chemicals and receptors known to be important in plasticity. For example, anatomical studies suggest that connections within the regions of the visual system that represent the central visual field are more strongly genetically specified, whereas connections within the portions of the visual system that represent the visual periphery contain redundant connections that can be shaped by experience over a longer developmental timecourse (Chalupa & Dreher, 1991). A molecular difference has also been observed between the two visual pathways. In cats and monkeys the dorsal pathway has a greater concentration of the Cat-301 antigen, a molecule hypothesized to play a role in stabilizing synaptic connections via experience-dependent plasticity (DeYoe et al., 1990; Hockfield, 1983). Moreover recent anatomical studies in nonhuman primates (Falchier et al., 2002, Falchier et al., 2002; Rockland & Ojima, 2003) and neuroimaging studies of humans (Eckert et al., 2008) report crossmodal connections between primary auditory cortex and the portion of primary visual cortex that represents the periphery (anterior calcarine sulcus). In addition there is considerable, though not unequivocal, evidence indicating that the dorsal pathway matures more slowly than the ventral pathway (Hickey, 1981; Hollants-Gilhuijs et al., 1998a; Hollants-Gilhuijs et al., 1998b; Packer et al., 1990). Further, in developmental studies using the

color and motion stimuli described above and in Armstrong et al. (2002), we observed that while children aged 6-19 years show responses to color stimuli that are very similar to adults, their ERPs to the motion stimuli are delayed in latency relative to those for adults (Coch, Skendzel et al., 2005, Mitchell & Neville, 2004) Together, these anatomical, chemical, and developmental mechanisms could render the dorsal pathway more modifiable by experience and more likely to display either enhanced or deficient processing.

In addition to enhanced dorsal pathway functioning we have recently observed that deaf (but not hearing) participants recruit a large, additional network of supplementary cortical areas when processing far peripheral relative to central flickering visual stimuli (Scott et al., 2003, see Fig 2). These include contralateral primary auditory cortex (Fig. 2). Studies of a mouse model of congenital deafness suggest that altered subcortical-cortical connectivity could account for such changes (Hunt et al., 2005). In deaf but not hearing mice the retina projects to the medial (auditory) geniculate nucleus as well as the lateral (visual) geniculate nucleus. In our study of deaf humans we also observe significant increases in anterior, primary visual cortex and regions associated with multisensory integration (STS), motion processing (MT/MT+), and attention (posterior parietal and anterior cingulate regions) (Dow et al., 2006; Scott et al., 2003; Scott et al., under review). In a separate study, 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) (Bavelier et al., 2000). 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 subjects. The findings of increased activation and effective connectivity between visual areas and areas important in attention suggest that the enhanced responsiveness to peripheral motion in deaf individuals may be in part linked to increases in attention (see below for further discussion).

## II. 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 (Rauschecker, 1998). Furthermore, animal and human studies of blindness have reported changes in the parietal cortex (i.e., dorsal pathway) as a result of visual deprivation (Hyvarinen & Linnankoski, 1981; Pascual-Leone et al., 2005; Weeks et al., 2000).

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 (Röder et al., 1996). 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 hearing participants (Neville et al.,

1983) 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 (Bishop & McArthur, 2004; Tallal & Piercy, 1974; Tallal, 1975; Tallal, 1976). 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 (Neville et al., 1993). This 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.

The mechanisms that give rise to greater modifiability of rapid auditory processing are as yet unknown. However, as mentioned above, some changes might be greater for magnocellular layers of the medial geniculate nucleus. For example, magnocells in both the lateral and medial geniculate nucleus are smaller than normal in dyslexia (Galaburda & Livingstone, 1993; Galaburda et al., 1994). Rapid auditory processing, including the recovery cycles of neurons, might also engage aspects of attention to a greater degree than other aspects of auditory processing. In the case of congenital blindness, changes in auditory processing may be facilitated by compensatory reorganization. A number of studies have confirmed that visual areas are functionally involved in non-visual tasks in congenitally blind adults (Cohen et al., 1999; Sedato et al., 1996). More recently studies have reported highly differentiated auditory language processing in primary visual cortex in congenitally blind humans (Burton et al., 2002; Röder et al., 2002). Thus, aspects of auditory processing that either depend upon or can recruit multimodal, attentional, or normally visual regions may show greater degrees of neuroplasticity. Parallel studies of animals have revealed information about mechanisms underlying this type of change. For example, in blind mole rats, normally transient, weak connections between the ear and primary visual cortex become stabilized and strong (Bavelier & Neville, 2002; Cooper et al., 1993; Doron & Wollberg, 1994; Heil et al., 1991).

### III. Language

It is reasonable to hypothesize that the same principles that characterize neuroplasticity of sensory systems—including different profiles, 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. For example, semantic violations in sentences elicit a bilateral negative potential that is largest around 400 ms following the semantic violation (Kutas & Hillyard, 1980; Neville et al., 1991; Newman et al., 2007). In contrast, syntactic violations elicit a biphasic response consisting of an early, left-lateralized anterior negativity (LAN) followed by a later, bilateral positivity, peaking over posterior sites ~600 ms after the violation (P600, Friederici, 2002; Neville et al., 1991). The LAN is hypothesized to index more automatic aspects of the processing of syntactic structure and the P600 to index later, more controlled processing of syntax associated with attempts to recover the meaning of syntactically anomalous sentences. 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) (Capek, 2004; Capek et al., under review). While spoken and signed language processing share a number of modality-independent 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 (Capek et al., 2004; Neville et al., 1998). 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).

We conducted a series of ERP studies to develop a neural index of one aspect of phonological processing: speech segmentation. By 100 ms after word onset, syllables at the beginning of a word elicit a larger negativity than acoustically similar syllables in the middle of the word (Sanders & Neville, 2003a). This effect has been demonstrated with natural speech and with synthesized nonsense speech in which only newly learned lexical information could be used for segmentation (Sanders et al., 2002). The early segmentation ERP effect resembles the effect of temporally selective attention, which allows for the preferential processing of information presented at specific time points in rapidly changing streams, and has also been shown to modulate early (100 ms) auditory ERPs (Lange et al., 2003; Lange & Roder, 2005; Sanders & Astheimer, in press). Thus, the neural mechanisms of speech segmentation may rely on the deployment of temporally selective attention during speech perception to aid in processing the most relevant rapid acoustic changes.

To the extent that language is comprised 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 (Johnson & Newport, 1989). In several studies we have examined whether delays in second language exposure are also associated with differences in the neural mechanisms underlying these different language subsystems. In one study, we compared the ERP responses to semantic and syntactic errors in English among Chinese/English bilinguals who were first exposed to English at different ages (Weber-Fox & Neville, 1996). 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 4-6 years. By comparison, the N400 response and the behavioral accuracy in detecting semantic anomalies were altered only in subjects who were exposed to English after 11-13 years of age. In studies of the effects of delayed second language acquisition on indices of speech segmentation, second language learners who were exposed to their second language late in life (> 14 years) show a delay in the ERP measure of speech segmentation when processing their second language (Sanders & Neville, 2003b).

Many deaf children are born to hearing parents and, due to 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 (Mayberry & Eichen, 1991; Mayberry, 1993; Mayberry et al., 2002; Mayberry, 2003). Recently studies have examined the effects of this delayed first language acquisition on

brain organization. We employed fMRI to examine whether congenitally deaf individuals who learned ASL later in life showed a different neural organization for ASL. In this study, we demonstrated that whereas the right angular gyrus is active when native signers process ASL, it is not in individuals who acquired ASL after puberty (Newman et al., 2002). Employing ERPs, we have also studied groups of deaf individuals who acquired ASL either from birth, from 2-10 years or between 11 and 21 years of age (Capek, 2004; Capek et al., in prep). In all three groups of participants, the N400 index of semantic processing displays the same amplitude, latency, and cortical distribution. However, the early anterior negativity thought to index more automatic aspects of syntactic processing is only evident in those who acquired ASL before the age of 10 years. These data suggest that, in contrast to semantic processing, aspects of syntactic processing are subject to maturational constraints that render them more vulnerable following delays in either first or second language acquisition.

Several lines of evidence suggest that language proficiency might be a key factor in predicting the variability observed in the neural substrates of syntax. For example, we have observed that the neural response to syntactic violations also differs among monolingual native English speakers who vary in language proficiency. Specifically, adults who score lower on standardized tests of grammatical knowledge show a less left-lateralized and more prolonged ERP response to grammatical violations (Pakulak et al., 2007; Pakulak & Neville, under review). In developmental studies as well, the neural response to known and unknown words and to syntactic anomalies is more strongly predicted by a child's language proficiency than by chronological age (Adamson et al., 1998; Adamson-Harris et al., 2000; Mills et al., 1993; Mills et al., 1997). Furthermore, the development of neural systems important for syntactic processing show a longer developmental time course than systems important for semantic processing (Hahne et al., 2004; Sabourin et al., 2007, and unpublished observations from data in our laboratory), again suggesting that systems with a longer developmental time course may be more modifiable during development.

#### IV. Attention

As noted above, 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 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 et al., 1992; Recanzone et al., 1993). Mere exposure is not enough. These data strongly suggest that attention is important in enabling neuroplasticity. Given this, and the central role of attention in learning more generally, we have conducted several studies on the development and neuroplasticity of attention.

In these studies, we examined the effects of sustained, selective attention on neural processing employing the 'Hillyard principle' i.e. while keeping the physical stimuli, arousal levels, and task demands constant. For example, competing streams of stimuli are presented (e.g., two different trains of auditory stimuli delivered to different ears), with participants alternating attention to one stream at a time in order to detect rare target events. By comparing neural activity to the same physical stimuli when attended versus ignored, the effects of selective attention can be ascertained. Studies with fMRI revealed that selective attention modulates the magnitude and extent of

cortical activation in the relevant processing areas (Corbetta et al., 1990). Complementary studies using the ERP methodology have clarified the time course of attentional modulation. These studies revealed that in adults, selective attention amplifies the sensori-neural response by 50-100% during the first 100 ms of processing (Hillyard et al., 1973; Hillyard et al., 2003; Luck et al., 2000; Mangun & Hillyard, 1990). This early attentional modulation is in part domain-general in that it is observed across multiple sensory modalities and in selection based on spatial, temporal, or other stimulus attributes. Moreover, in between-group and change-over-time comparisons, ERPs can separately index processes of signal enhancement (ERP amplitude gains for attended stimuli) and distracter suppression (amplitude reductions for unattended stimuli).

In a number of studies we have documented that neuroplasticity in the early neural mechanisms of selective attention, as in other neural systems, shows considerable specificity. In the case of adults born deaf, employing ERPs and fMRI, we observed enhancements of attention that were specific to the peripheral, but not central, visual field (Bavelier et al., 2000; Bavelier et al., 2001; Neville & Lawson, 1987b). In parallel studies of auditory spatial attention among congenitally blind adults, we have observed similar specificity. When attending to central auditory space, blind and sighted participants displayed similar localization abilities and ERP attention effects. In contrast, in the periphery, blind participants were superior to sighted controls at localizing sounds in peripheral auditory space, and ERPs revealed a sharper tuning of early spatial attention mechanisms (the N1 attention effect) (Röder et al., 1999). In a recent study of adults blinded later in life, we observed possible limits on the time periods during which these early mechanisms of attention are enhanced (Fieger et al., 2006). Whereas adults blinded later in life showed similar behavioral improvements in peripheral auditory attention, these improvements were mediated by changes in the tuning of later ERP indices of attention, several hundred ms after stimulus onset (i.e. P300). There were no group differences in the early (N1) attention effects. If the early neural mechanisms of selective attention can be enhanced after altered experience, it is possible that, as with other systems that display a high degree of neuroplasticity, attention may be particularly vulnerable during development. In line with this hypothesis, recent behavioral studies suggest that children at-risk for school failure, including those with poor language or reading abilities or from lower socioeconomic backgrounds, exhibit deficits in aspects of attention including filtering and noise exclusion (Atkinson, 1991; Cherry, 1981; Farah et al., 2006; Lipina et al., 2005; Noble et al., 2005; Sperling et al., 2005; Stevens, Sanders, Andersson et al., 2006; Ziegler et al., 2005). These attentional deficits span linguistic and nonlinguistic domains within the auditory and visual modalities, suggesting that the deficits are both domain general and pansensory. In order to determine whether these attentional deficits can be traced to the earliest effects of attention on sensorineural processing, we have recently used ERPs to examine the neural mechanisms of selective attention in typically developing, young children and in groups of children at-risk for school failure.

These studies were modeled after those we and others have used with adults (Hillyard et al., 1973; Neville & Lawson, 1987a; Röder et al., 1999; Woods, 1990). The task was designed to be difficult enough to demand focused selective attention, while keeping the physical stimuli, arousal levels, and task demands constant. Two different children's stories were presented concurrently from speakers to the left and right of participant. Participants were asked to attend to one story and ignore the other.

Superimposed on the stories were probe stimuli to which ERPs were recorded. Adults tested with this paradigm showed typical N1 attention effects (Coch, Sanders et al., 2005). Children, who showed a different ERP morphology to the probe stimuli, also showed early attentional modulation within the first 100 ms of processing. This attentional modulation was an amplification of the broad positivity occurring in this time window. In a later study (Sanders et al., 2006), we found that this attention effect was complete by 200 ms in older children age 6-8 years but prolonged through 300 ms in children age 3-5. These data suggest that with sufficient attentional cues, children as young as three years of age are able to attend selectively to an auditory stream and that doing so alters neural activity within 100 ms of processing.

We have employed this paradigm to examine the timing and mechanisms of selective auditory attention in children with specific language impairment (SLI) aged six to eight years and typically developing (TD) control children matched for age, gender, non-verbal IQ, and socio-economic status (SES) (Stevens, Sanders, & Neville, 2006). As shown in Figure 3a, c, by 100 ms, typically developing children in this study showed an amplification of the sensori-neural response to attended as compared to unattended stimuli, just as observed in our larger samples of typically developing children. In contrast, children with SLI showed no evidence of sensori-neural modulation with attention, despite behavioral performance indicating that they were performing the task as directed (Fig. 3, b, d). Moreover, the group differences were specific to signal enhancement (Fig. 4 left).

In a related line of research, we examined the neural mechanisms of selective attention in children from different socioeconomic backgrounds. Previous behavioral studies indicated that children from lower socioeconomic backgrounds experience difficulty with selective attention, and particularly in tasks of executive function and in those tasks that require filtering irrelevant information or suppressing prepotent responses (Farah et al., 2006; Lupien et al., 2001; Mezzacappa, 2004; Noble et al., 2005; Noble et al., 2007). Using the same selective auditory attention ERP task described above, we observed differences in the neural mechanisms of selective attention in children from different socioeconomic backgrounds (Stevens, Lauinger et al., in press). Specifically, children whose mothers had lower levels of education (no college experience) showed reduced effects of selective attention on neural processing compared to children whose mothers had higher levels of education (at least some college) (Fig. 5). These differences were related specifically to a reduced ability to filter irrelevant information (i.e., to suppress the response to ignored sounds) (Fig. 4 right) and could not be accounted for by differences in receptive language skill. Thus, the mechanism implicated in attention deficits in children from lower socioeconomic backgrounds (i.e., distractor suppression) was not the same as the mechanism implicated in children with SLI, who showed a deficit in signal enhancement of stimuli in the attended channel (Stevens, Sanders, & Neville, 2006). Similar results have been reported by other research groups (D'Angiulli et al., 2008). Taken together, these studies point to the two sides of the plasticity of early mechanisms of attention, which show both enhancements and vulnerabilities in different populations.

Several mechanisms might underlie the plasticity of attention. Whereas the research described above focused on sustained, selective attention, research in cognitive science and cognitive neuroscience has also identified several different subsystems, or components of attention (Coull et al., 1996; Raz & Buhle, 2006; Shipp, 2004). These components of attention depend upon different neural substrates and neurotransmitters (Bush et al., 2000; Gomes et al., 2000; Posner & Petersen, 1990) and mature along

different time tables (Andersson & Hugdahl, 1987; Doyle, 1973; Geffen & Wale, 1979, Hiscock & Kinsbourne, 1980, Pearson & Lane, 1991; Rueda, Fan et al., 2004; Rueda, Posner et al., 2004; Schul et al., 2003). Sustained, selective attention shows a particularly long time course of development. Both the abilities to selectively attend to relevant stimuli and to successfully ignore irrelevant stimuli improve progressively with increasing age across childhood (Cherry, 1981; Geffen & Sexton, 1978; Geffen & Wale, 1979; Hiscock & Kinsbourne, 1980; Lane & Pearson, 1982; Maccoby & Konrad, 1966; Sexton & Geffen, 1979; Zukier & Hagen, 1978). Further, there is some evidence that background noise creates greater interference effects for younger children as compared to adolescents or adults (Elliott, 1979; Ridderinkhof & van der Stelt, 2000). In a review of both behavioral and ERP studies of the development of selective attention, Ridderinkhof and van der Stelt (2000) proposed that the abilities to select among competing stimuli and to preferentially process more relevant information are essentially available in very young children, but that the speed and efficiency of these behaviors and the systems contributing to these abilities improve as children develop. Additionally, since the key sources of selective attention within the parietal and frontal lobes constitute parts of the dorsal pathway, similar chemical and anatomical factors noted in the section on vision may contribute to the plasticity of attention in a similar way. In addition, recent evidence suggests that there are considerable genetic effects on attention (Bell et al., 2008; Fan et al., 2003; Posner et al., 2007; Rueda et al., 2005) and that these may also be modified by environmental input epigenetically (Bakermans-Kranenberg et al., 2008; Sheese et al., 2007; unpublished observations from our lab).

## V. Interventions

As described above, selective attention influences early sensory processing across a number of domains. In our most recent research, we have been investigating the possibility that attention itself might be trainable, and that this training can impact processing in a number of different domains. Indeed, in his seminal work, *Principles of Psychology*, William James raised the idea of attention training for children, proposing that this would be “*the education par excellence*” (James, 1890, italics original). While James went on to say that such an education is difficult to define and bring about, attention training has recently been implemented in curricula for preschool and school-age children (Bodrova & Leong, 2007; Chenault et al., 2006; Diamond et al., 2007; Rueda et al., 2005). These programs are associated with improvements in behavioral and neurophysiological indices of attention, as well as in measures of academic outcomes and nonverbal intelligence. Furthermore, one program showed that attention training translated to increased benefits of a subsequent remedial writing intervention for adolescents with dyslexia (Chenault et al., 2006).

Recent proposals suggest that some interventions designed to improve language skills might also target or train selective attention (Gillam, 1999; Gillam, Loeb et al., 2001; Gillam, Crofford et al., 2001; Hari & Renvall, 2001). We have tested this hypothesis in a series of intervention studies. In this research, we have documented changes in the neural mechanisms of selective attention following training in typically developing children, as well as children with language impairment or at-risk for reading failure (Stevens, Fanning et al., 2008, Stevens, Harn et al., in press). In all cases, increases in the effects of attention on sensorineural processing were accompanied by behavioral changes in other domains that were also targeted by the training programs, including language and preliteracy skills. These data suggest that modifications in behavior can arise alongside changes in the early neural mechanisms of attention.

In one study, we examined whether six weeks of high-intensity (100 min/day) training with a computerized intervention program designed to improve language skills would also influence neural mechanisms of selective auditory attention previously shown to be deficient in children with SLI (Stevens, Fanning et al., 2008). Before and after training (or a comparable delay period for a no treatment control group), children completed standardized language assessments and the ERP measure of selective auditory attention described above. Relative to the no treatment control group, both children with SLI and typically developing children receiving training showed increases in standardized measures of receptive language. In addition, children receiving training showed larger increases in the effects of attention on neural processing following training relative to the control group, and these changes were specific to changes in signal enhancement of attended stimuli (Fig. 6).

In a second study, we examined the neural mechanisms of selective attention in kindergarten children who were either on-track in preliteracy skills or at-risk for reading failure. They were studied at the beginning of and following the first semester of kindergarten (Stevens, Currin et al., 2008; Stevens, Harn et al., in press). The at-risk group also received supplemental instruction with a previously-validated reading intervention (Simmons et al., 2003; Simmons et al., 2007). Behaviorally, the at-risk group showed improved performance on several preliteracy measures, raising their performance close to the on-track group by the end of the year. At the start of kindergarten, the at-risk group displayed reduced effects of attention on sensorineural processing compared to the on-track group. Following training, this difference between groups disappeared, with the at-risk group showing increased effects of attention on sensorineural processing (Fig. 7).

fMRI data from the same kindergarten children further supported the role of attentional changes in successful language or reading interventions (Yamada et al., 2008; Yamada et al., under review). Hemodynamic responses to visually presented letters or false font stimuli (presented in separate blocks) were examined. Participants indicated when the same letter or false font stimulus was repeated in two successive trials (i.e., a 1-back task). Consistent with previous research on reading-related networks in fluent readers, adults recruited a left temporo-parietal region during this task (Fig. 8a). At the start of kindergarten, on-track children recruited bilateral temporo-parietal regions, whereas children at-risk for reading failure did not show greater recruitment of any brain regions for letters versus false font stimuli (Fig. 8b). Following 3 months of kindergarten and, for children at-risk for reading failure, supplemental reading instruction, both groups showed changes in reading circuits toward more adult-like patterns, though the at-risk group showed a less mature pattern of activation (Fig. 8c). Interestingly, following a semester of kindergarten, the at-risk group showed greater activation than the on-track group of supplemental frontal regions, including the anterior cingulate cortex. (Fig. 8). This suggested that changes in the neural circuits for reading in response to intervention also involved the recruitment of additional neural resources related to attention.

In a related line of research, we have also begun studies that train parents of children from lower socioeconomic backgrounds. Across eight weekly, small-group sessions, parents learn evidence-based strategies to improve communication with their children, promote children's critical thinking skills, and decrease family stress. We have compared the pre- to post-training changes in this group of parents and their children to changes in a matched control group randomly assigned not to receive the

intervention. To date the parent training appears very promising (Fanning, 2007; Fanning et al., 2008; Fanning et al., under review). Relative to the control group, parents in the intervention group show larger decreases in self-reported stress related to parenting challenges. When interacting with their children, their language becomes more child-directed (e.g., they allow more opportunities for the child to talk and to guide the interaction). In addition there are large changes in the children themselves. Children whose parents completed the training show large and significant increases in standardized measures of language, nonverbal IQ, memory, and attention compared to children whose parents are randomly assigned not to receive the intervention. We are continuing to assess the parent training program by looking at the effects of the training on attention and language-related ERPs. We are following children longitudinally to see whether improvements persist and generalize to school performance. In addition, we are adapting the parent training program to include a stronger focus on developing children's attention and self-regulation skills.

Finally, recent studies have linked variability in polymorphisms of genes that influence the production, metabolism, and transport of neurotransmitters important in attention to variability in behavioral, ERP, and fMRI indices of attention (Bell et al., 2008; Fan et al., 2003; Greenwood & Parasuraman, 2003). For example the 3 repeat allele of the MAOA gene is associated with reductions in language and cognition including executive attention and to reductions in our ERP attention effects and activation of ACC on fMRI compared to the 4 repeat allele (Bell et al., 2008; Fan et al., 2003). The long-long allele of the serotonin transporter gene and the 7 repeat allele of the DRD4 gene are associated with increased rates of ADHD and reduction of our ERP attention effects (Bell et al., 2008; Fan et al., 2003; Parasuraman et al., 2005; Rueda et al., 2005; Savitz et al., 2006). However, recent studies suggest that such genetic effects display plasticity that is dependent on and modified by environmental input including parenting quality, parental interventions, and small group interventions (Bakermans-Kranenberg & Van Ijzendoorn, 2006; Bakermans-Kranenberg et al., 2008; Sheese et al., 2007 and our unpublished observations). Thus gene x environment interactions and epigenetic mechanisms similar to those operating in animal studies (Kondo et al., 2008; Meaney, Hensch this volume; Suomi, 2003; Suomi, 2006) likely play a role in determining the different profiles of human neuroplasticity as well.

## VI. Conclusions

The research described in this chapter has illustrated the variable degrees and timeperiods 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 profiles and mechanisms of neuroplasticity as a point of departure in the development of training and intervention programs. Our growing 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.

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## Figure Legends

### Figure 1

Performance on two visual tasks for deaf participants (grey bars) and dyslexic participants (white bars) relative to matched control groups. The zero line represents performance of the respective control groups. Upper panel shows data on a central visual field contrast sensitivity task, in which neither deaf nor dyslexic participants differed from matched controls. Lower panel shows data from a peripheral visual field motion detection task, in which deaf participants showed enhancements ( $P < .001$ ) and dyslexic participants showed deficits ( $P < .01$ ) relative to matched controls. Data from Stevens & Neville (2006).

### Figure 2

Deaf and hearing participants completed a visual retinotopy experiment which included mapping of far peripheral visual space. The data show regions where activation was greater in deaf versus hearing participants in response to more peripheral visual stimuli presented in two distinct experiments ( $45-56^\circ$  vs.  $11-23^\circ$  and  $11-15^\circ$  vs  $2-7^\circ$ ). Significant clusters included contralateral auditory cortex, STS, MT,

anterior visual cortex, IPS, and anterior cingulate.

### Figure 3

Grand average event-related potentials (ERPs) for attended and unattended stimuli, (a) in typically developing children ( $P = .001$ ) and (b) in children with specific language impairment ( $P > 0.4$ ). Voltage map of the attention effect (Attended-Unattended) shows (c) in typically developing children a large, broadly distributed effect and (d) in children with specific language impairment no modulation with attention. Data from Stevens, et al (2006). Image reproduced with permission from Brain Research.

### Figure 4

Mean amplitude of the ERP from 100-200 msec of responses to unattended and attended probes. Error bars represent standard error of the mean. Left panel shows data from typically developing children (TD) and children with specific language impairment (SLI). The two groups did not differ in the magnitude of response to unattended stimuli. However, typically developing children showed a larger amplitude response (i.e., better signal enhancement) than children with SLI to attended stimuli. Right panel shows data from children from higher versus lower socioeconomic backgrounds. Children from different socioeconomic backgrounds did not differ in the magnitude of response to attended stimuli. However, children from lower socioeconomic backgrounds showed a larger response (i.e., poorer filtering) to unattended stimuli compared to children from higher socioeconomic backgrounds. Data from Stevens et al, 2006, Brain Research and Stevens, et al, in press, Developmental Science.

### Figure 5

Grand average evoked potentials for attended and unattended stimuli in children from higher socioeconomic backgrounds (upper panel) and lower socioeconomic backgrounds (lower panel). The effect of attention on sensorineural processing was significantly larger in children from higher socioeconomic backgrounds ( $P = .001$ ). Data from Stevens, et al, in press, Developmental Science.

### Figure 6

ERP responses to attended and ignored auditory stimuli in typically developing (TD) children and children with specific language impairment (SLI) before and after six weeks of daily, 100-minute computerized language training. Grand average evoked potentials for attended and unattended stimuli are collapsed across linguistic and nonlinguistic probes. Voltage maps shows magnitude and distribution of the attention effect (attended - unattended) during the 100-200 ms time window. Following training, both children with SLI ( $P < .05$ ) and typically developing children ( $P < .1$ ) showed evidence of increased effects of attention on sensorineural processing. These changes were larger than those made in a no-treatment control group ( $P < .01$ ), who showed no change in the effects of attention on sensorineural processing when retested after a comparable time period ( $P = 0.96$ ).

### Figure 7

Grand average ERP waveforms from the selective auditory attention paradigm show the effects of attention on sensorineural processing in kindergarten children of diverse

early reading ability across the first semester of kindergarten. Top row shows data from pretest and bottom row shows data from posttest for five-year-old kindergarten children on-track (OT) in early literacy skills or at-risk (AR) for reading difficulty. The OT group received eight weeks of kindergarten between pretest and posttest. The AR group received eight weeks of kindergarten with 45 minutes of daily, supplemental instruction with the Early Reading Intervention (ERI). Voltage map indicates the magnitude and distribution of the attention effect (Attended-unattended). Changes in the effects of attention differed from pretest to posttest in the two groups ( $P < .05$ ), with the OT group showing no change ( $P = .92$ ) and the AR group showing a significant increase in the attention effect ( $P < .01$ ). At pretest, the OT group tended to have a larger attention effect than the AR group ( $P = .06$ ). At posttest, the AR group had a nonsignificantly larger attention effect than the OT group ( $P = .17$ ).

### Figure 8

fMRI activations for Letter > False Font while performing a 1-back task in adults and kindergarten children of diverse reading ability across the first semester of formal reading instruction. (a) Adults performing the task displayed activation in classic left temporo-parietal regions. (b) In contrast, at the beginning of kindergarten, children on-track in early literacy skills (upper panel) showed bilateral temporo-parietal activation and children at-risk for reading difficulty (lower panel) showed no regions of greater activation. (c) Following one semester of kindergarten and, for children in the at-risk group, daily supplemental instruction with the Early Reading Intervention, on-track children showed left-lateralized activation in temporo-parietal regions and at-risk children showed bilateral temporo-parietal activation and large activation of frontal regions, including the ACC. The left hemisphere is displayed on the left. In the upper left corner are example stimuli.

Figure 1

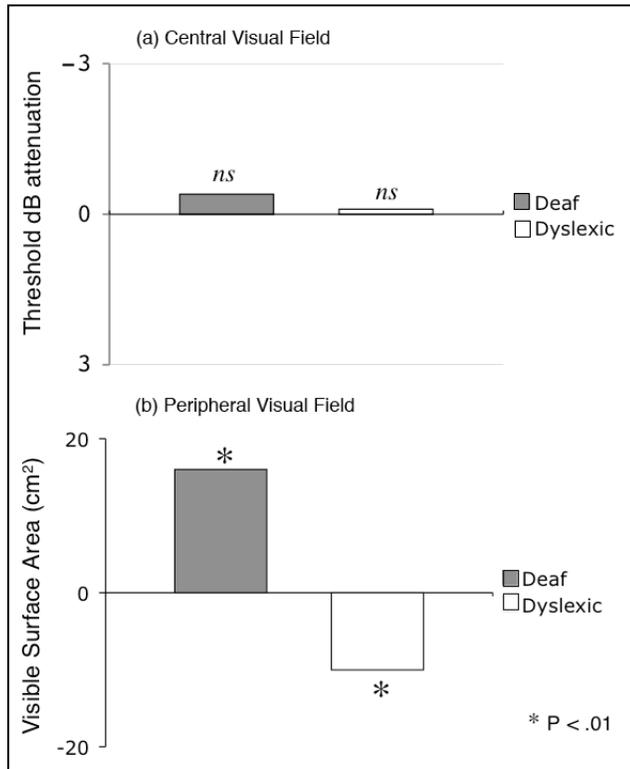


Figure 2

Deaf greater than hearing: Periphery (right visual field)

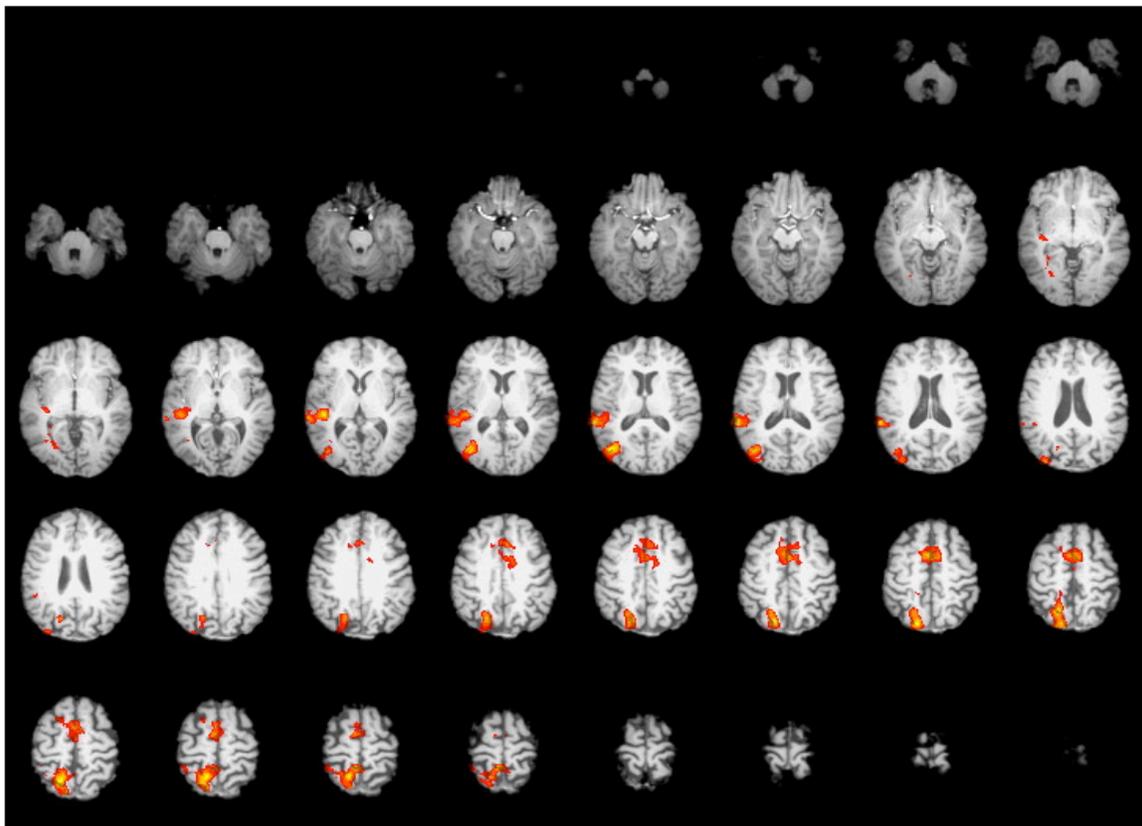


Figure 3

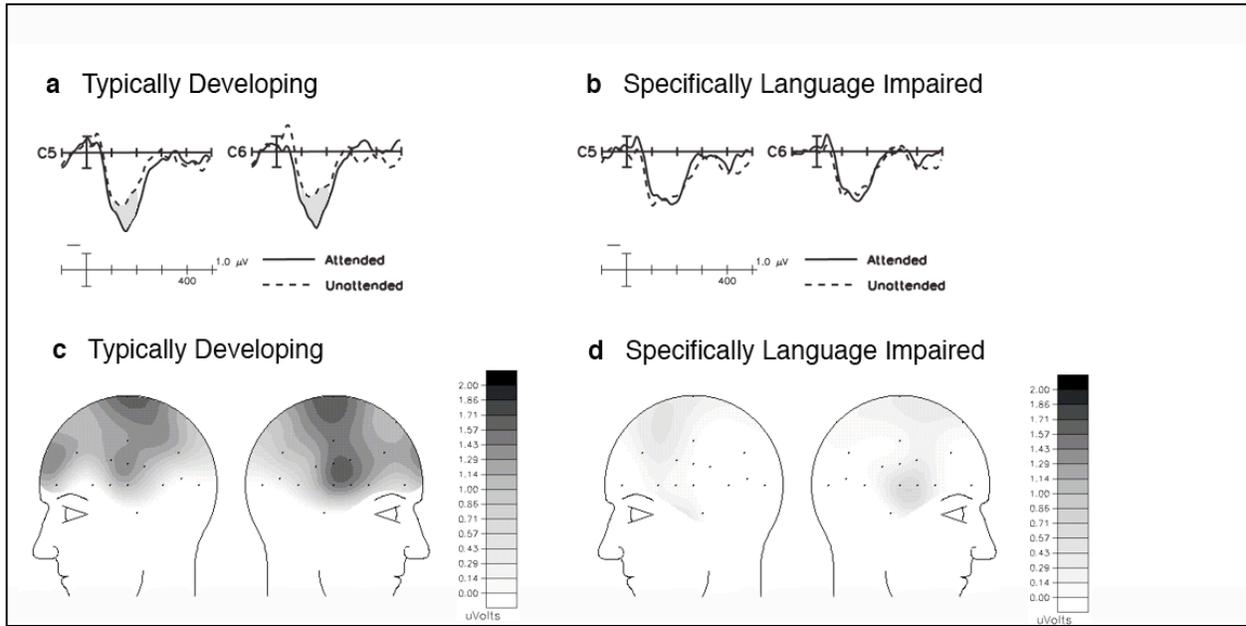


Figure 4

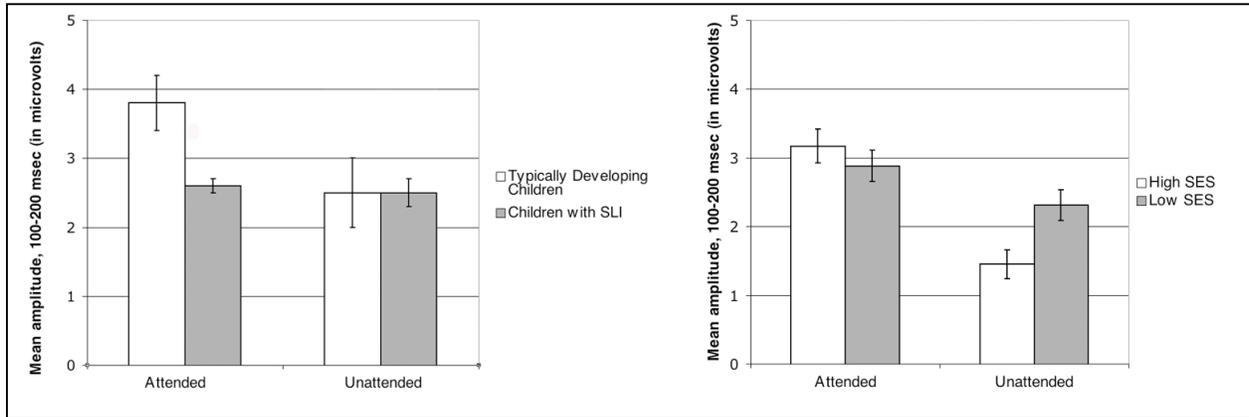


Figure 5

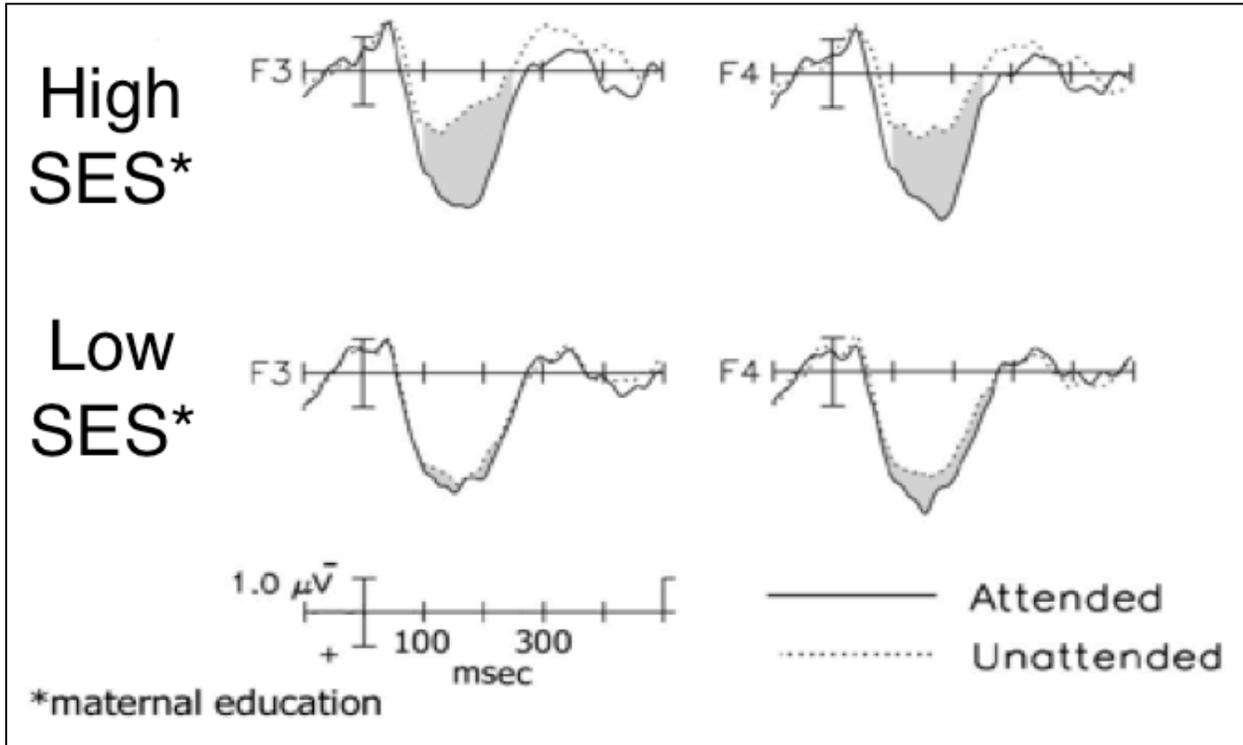


Figure 6

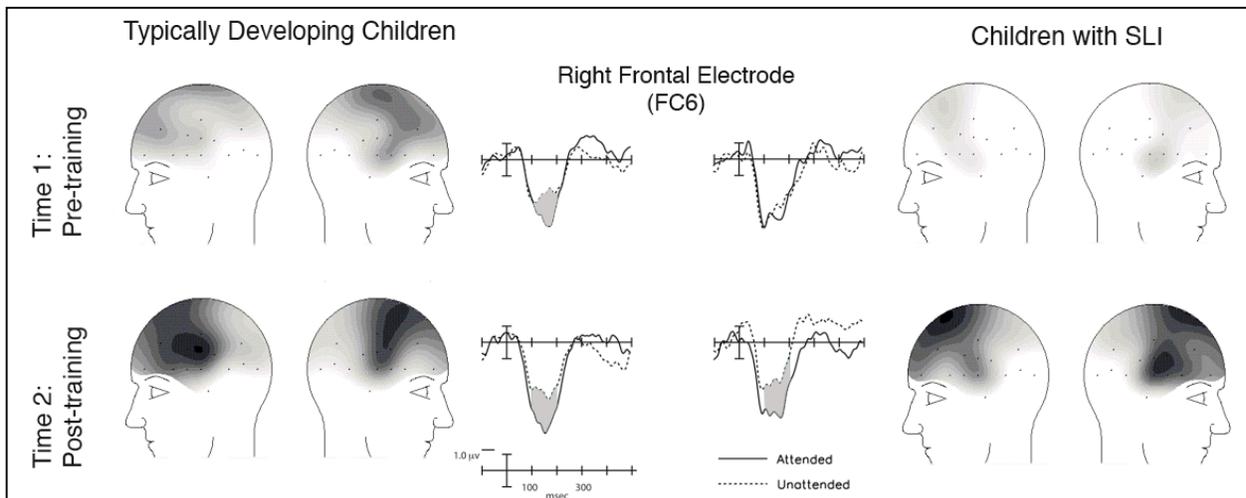


Figure 7

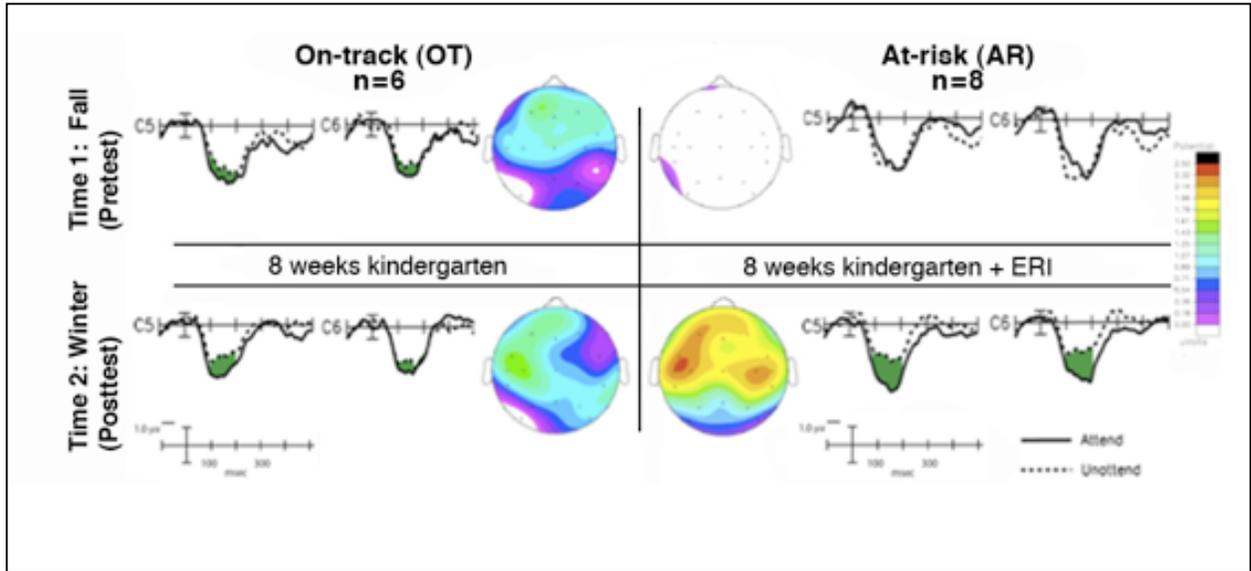


Figure 8

