Specificity of Experiential Effects in Neurocognitive Development

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THE NEW COGNITIVE NEUROSCIENCES

Fifth Edition

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

2013

Abstract

Here, we report research on the neuroplasticity of different subsystems within vision, audition, sensory integration, language, and attention. In each section, we note different profiles of plasticity observed in different subsystems within the domain, situations in which enhancements versus deficits are observed, and likely mechanisms contributing to these different profiles of plasticity. A final section describes our studies that test 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.

For several years we have employed psychophysics, electrophysiological (ERP), and magnetic resonance imaging (MRI) techniques to study the development and neuroplasticity 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 stages of cognitive development. Here, we review our research on the neuroplasticity of different brain systems and subsystems. As detailed in the sections that follow, in each of the domains examined in this research 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.

- Neuroplasticity within a system acts as a double-edged sword, conferring the possibility for *either* enhancement or deficit.

- Multiple mechanisms both support and constrain the ability to modify different brain systems and subsystems, with the most malleable systems generally displaying longer developmental trajectories, higher levels of redundant connectivity, and a greater concentration of neurochemicals, including CAT301 and BDNF important in neuroplasticity.

In the sections that follow, we describe our research on neuroplasticity within visual, auditory, sensory integration, language, and attention systems. In each section, we note different profiles of plasticity that are system and context dependent and in which enhancements versus deficits are observed. We also propose likely mechanisms contributing to these different profiles of plasticity. A final section describes our studies that test the hypothesis, raised by this basic research on human neuroplasticity, that interventions that target the most plastic, and thus potentially most vulnerable, neurocognitive systems can protect and enhance children with, or at risk for, developmental deficits.

I. Vision

The primate visual system contains multiple distinct visual areas, with a gross segregation of cortical visual processing into dorsal and ventral streams that project respectively from V1 toward posterior parietal cortex and ventrally toward the temporal cortex (Grill-Spector & Malach, 2004; Ungerleider & Haxby, 1994). In our research, we observe that aspects of vision

and attention mediated by the dorsal pathway – including motion perception, peripheral vision, and selective attention – are most modifiable with altered experience, showing both enhancements and deficits in special populations.

In one line of research, we examined changes in visual processing in congenitally, genetically deaf adults. By virtue of an increased reliance on vision, we hypothesized that deaf adults would exhibit enhancements in visual processing. Indeed, our studies revealed improvements in some – but not all – aspects of vision in these deaf adults. For example, congenitally deaf individuals have superior motion detection than hearing individuals for peripheral visual stimuli (Neville & Lawson, 1987b; Neville, Schmidt, & Kutas, 1983; Stevens & Neville, 2006). These improvements are accompanied by increases in the amplitudes of early visual event-related potentials (ERPs) for peripheral visual stimuli, as well as increased functional magnetic resonance imaging (fMRI) activation in motion-sensitive middle temporal (MT) and middle superior temporal (MST) areas (Armstrong, Hillyard, Neville, & Mitchell, 2002; Bavelier et al., 2001; Bavelier et al., 2000; Neville & Lawson, 1987b; Neville et al., 1983). In contrast, we observe no differences between deaf and hearing adults in tasks tapping ventral pathway functions, including central visual field tasks and isoluminant color processing (Armstrong et al., 2002; Bavelier et al., 2001; Bavelier et al., 2000; Neville & Lawson, 1987b; Neville et al., 1983; Stevens & Neville, 2006).

If neuroplasticity indeed acts as a double-edged sword, conferring both the potential for a system to be enhanced or to show deficits, one might predict that dorsal visual functions would– under different conditions – be selectively vulnerable to *deficit*. This is indeed the case. For example, several studies report that visual processing mediated by the dorsal (but not ventral) pathway shows deficits in many developmental disorders, including Autism, Williams, and Fragile X syndromes, as well as in individuals with reading or language impairments (Atkinson, 1992; Atkinson et al., 1997; Cornelissen, Richardson, Mason, Fowler, & Stein, 1995; Demb, Boynton, Best, & Heeger, 1998; Eden et al., 1996; Everatt, Bradshaw, & Hibbard, 1999; Hansen, Stein, Orde, Winter, & Talcott, 2001; Lovegrove, Martin, & Slaghuis, 1986; Sperling, Lu, Manis, & Seidenberg, 2003; Talcott, Hansen, Assoku, & Stein, 2000).

Interestingly, the literatures showing enhancements and deficits in dorsal pathway visual function have developed largely in parallel, with different experimental paradigms employed in each literature. To examine whether parallel enhancements and deficits could be observed in dorsal pathway function, we have used the same visual processing tasks in congenitally deaf adults (hypothesized to show enhancements) and dyslexic adults (hypothesized to show deficits), as shown in Figure 1. In this study we observe the two sides of plasticity, using the same experimental paradigm to show enhancements in deaf adults and deficits in adults with dyslexia for dorsal visual pathway tasks, with no difference for either group in visual tasks relying on the ventral pathway (Stevens & Neville, 2006).

Taken together, these data suggest that the dorsal visual pathway exhibits 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 individuals with some developmental disorders). The dorsal pathway is likely more developmentally labile due to subsystem differences in rate of maturation, extent and timing of redundant connectivity, and presence of neurochemicals and receptors known to be important in plasticity (for a review, see Bavelier & Neville, 2002). For example, there is considerable, though not unequivocal, evidence indicating that the dorsal pathway matures more slowly than the ventral pathway (Coch, Skendzel, Grossi, & Neville, 2005; Hickey, 1981; Hollants-Gilhuijs, Ruijter, & Spekreijse,

1998a, 1998b; Mitchell & Neville, 2004; Packer, Hendrickson, & Curcio, 1990). Anatomical studies also suggest that connections within regions of the visual system that represent the central visual field are more strongly genetically specified and display fewer redundancies, whereas connections within the portions of the visual system that represent the visual periphery contain more redundant connections that can be shaped by experience over a longer developmental time course (Chalupa & Dreher, 1991). Moreover, anatomical studies in nonhuman primates (Falchier, Clavagnier, Barone, & Kennedy, 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 our own laboratory, we observe 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, including regions associated with auditory and visual processing (A1 and V1), multisensory integration (STS), motion processing (MT/MT+), and attention (posterior parietal and anterior cingulate regions) (Scott, Dow, Karns, Stevens, & Neville, in prep). In sum, the anatomical, neurochemical, and developmental mechanisms mentioned above could render particular aspects of vision more modifiable by experience and likely to display either enhanced or deficient processing.

II. Audition

To test whether the specificity of plasticity observed in the visual system generalizes to other sensory systems, we have conducted studies on 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 have shorter conduction times than the smaller (parvo) cells, and evidence suggests that there may be dorsal and ventral auditory processing streams with different functional specializations (Rauschecker, 1998). 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, Teder-Salejarvi, et al., 1999). Congenitally blind participants were faster at detecting the targets 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 dual nature of the plasticity observed in the dorsal visual pathway, the processing of rapidly presented acoustic information, which is enhanced in the blind, shows deficits in some developmental disorders (Bishop & McArthur, 2004; Tallal, 1975, 1976; Tallal & Piercy, 1974). Using ERPs, we have observed in two studies of children with specific language impairment (SLI) that the amplitude of auditory evoked potentials were smaller (i.e., more refractory) than in controls, but only at short interstimulus intervals (Neville, Coffey, Holcomb, & Tallal, 1993; Stevens, Paulsen, Yasen, Mitsunaga, & Neville, 2012). 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 different 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

divisions of the medial geniculate nucleus. For example, magno, but not parvo, cells in both the lateral and medial geniculate nucleus are smaller than normal in dyslexia (Galaburda & Livingstone, 1993; Galaburda, Menard, & Rosen, 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 confirm that primary and secondary visual areas are functionally involved in non-visual tasks in congenitally blind adults (Burton et al., 2002; Cohen, Weeks, Celnik, & Hallett, 1999; Röder, Stock, Bien, Neville, & Rösler, 2002; Sedato et al., 1996). In addition, parallel studies in animals reveal information about mechanisms underlying crossmodal plasticity. For example, in blind mole rats, normally transient, weak connections between the ear and primary visual cortex become stabilized and more pronounced (Bavelier & Neville, 2002; Cooper, Herbin, & Nevo, 1993; Doron & Wollberg, 1994; Heil, Bronchti, Wollberg, & Scheich, 1991). Thus, portions of the auditory network that either depend upon or can recruit multimodal, attentional or normally visual regions may show greater degrees of neuroplasticity.

III. Sensory Integration

The above discussion suggests that, in some cases, plasticity might be related to the interactions and integration among different sensory systems. Most research examining cross-modal plasticity in congenitally deaf adults has focused exclusively on vision. In the visual domain, it is unclear whether primary auditory cortex shows cross-modal plasticity since the studies have employed methods that poorly localize Heschl's gyrus. Only a few studies have examined the somatosensory modality (Auer, Bernstein, Sungkarat, & Singh, 2007; Lavänen, Jousmäki, & Hari, 1998). These somatosensory studies implicate Heschl's gyrus in cross-modal plasticity but are also limited in anatomical precision. A third study, using MEG and fMRI in a single congenitally deaf individual, found neither visual nor somatosensory responses in deaf auditory cortex (Hickok et al., 1997).

A large literature on developmental disorders reports deficits in multisensory integration (e.g., see Foss-Feig et al., 2010; Hairston, Burdette, Flowers, Wood, & Wallace, 2005; Iarocci & McDonald, 2006). We recently tested the hypothesis raised by these results—i.e. that multisensory integration is a process that displays considerable neuroplasticity and may, therefore, be capable of large enhancements in the deaf. We examined whether visual, somatosensory, and bimodal processing is altered in congenitally deaf adult humans by quantifying fMRI signal change within anatomically defined Heschl's gyrus and in superior-temporal cortex in individual subjects (Karns, Dow, & Neville, 2012). We found that deaf adults did recruit Heschl's gyrus slightly for processing visual stimuli, but to a much larger extent for somatosensory processing and visual-somatosensory stimuli. Importantly, this cross-modal neuroplasticity had functional consequences, namely altered perception in deaf individuals. Only the congenitally deaf adults in our study reported a somatosensory double-flash illusion, a visual percept induced by a somatosensory stimulus. However, this somatosensory recruitment was not constant across deaf individuals. We found that those individuals with the strongest response to somatosensory stimuli in Heschl's gyrus also saw the somatosensory-induced double flash illusion more frequently. This research shows that in congenital deafness, even primary sensory cortices can be recruited to process other sensory modalities. Interestingly, it has recently been proposed that multisensory integration and attention are tightly interconnected (Talsma,

Senkowski, Soto-Faraco, & Woldorff, 2010), suggesting that attention may facilitate or enable plasticity in multisensory processing.

IV. 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. Indeed, as in the sensory systems, language exhibits a number of distinct subsystems, with non-identical neural networks mediating the processing of, for example, semantics, syntax, and speech segmentation. As an example, when sentences contain a semantic (as opposed to syntactic) violation, ERPs to the semantic violation reveal a bilateral negative potential that is largest around 400 ms (N400) (Kutas & Hillyard, 1980; Neville, Nicol, Barss, Forster, & Garrett, 1991; Newman, Ullman, Pancheva, Waligura, & Neville, 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 (see below for new evidence on this) and the P600 to index later, more controlled processing of syntax associated with attempts to recover the meaning of syntactically anomalous sentences. In the case of speech segmentation, there are also distinct ERP responses to word-initial as compared to word-medial syllables. 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 (Astheimer & Sanders, 2009; Sanders & Neville, 2003a; Sanders, Newport, & Neville, 2002). Below, we examine the degree to which these three subsystems – semantics, syntax, and speech segmentation – display neuroplasticity with altered experience.

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). Similarly, in studies of Chinese/English bilinguals who were first exposed to English at different ages the neural systems associated with syntactic processing are vulnerable to differences, with early delays in age of acquisition. On the other hand the neural systems associated with semantic processing are more robust against delays in age of acquisition (Weber-Fox & Neville, 1996). We also observe atypical ERP effects of speech segmentation among late-learners when processing their second language (Sanders & Neville, 2003b). However, studies of bilingual participants suffer from two limitations: (1) the difficulty of separating out effects of age of acquisition from language proficiency, and (2) the difficulty of assessing whether any observed differences in neural organization are due to delays in acquisition as compared to interference from a first-learned language. In related research, we have addressed each of these issues.

In one recent study, we examined the effects of delayed age of acquisition in a group of high-proficiency German-English bilingual participants, in which proficiency was equivalent to that of native English speakers. However, as shown in Figure 2, even in this proficiency-matched group later age of acquisition was associated with atypical ERP responses to syntactic violations, and in particular an absence of the early LAN effect (Pakulak & Neville, 2011). This suggests that age of acquisition can influence the neural systems recruited during language processing, independent of language proficiency. However, at the same time, we have – in separate studies –

observed effects of language proficiency on the neural systems used for language processing, even among native speakers (Pakulak & Neville, 2010). Specifically, whereas high proficiency native speakers show the typical biphasic LAN/P600 response to syntactic violations, native speakers of lower proficiency show a less spatially and temporally focal early neural response, as well as a reduced amplitude P600 (see Figure 2). Indeed, 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, Mills, Appelbaum, & Neville, 1998; Adamson-Harris, Mills, & Neville, 2000; Mills, Coffey-Corina, & Neville, 1993, 1997). These data suggest that both age of acquisition and language proficiency affect the neural systems used during language processing.

To address whether altered neural organization in late bilinguals is due to age of acquisition versus interference of a first-learned language, we have studied a unique group of individuals: deaf signers who acquired sign language late in life. Many deaf children are born to hearing parents and, due to their limited access to spoken language, do not have full access to a first language until exposed to a signed language, which often occurs very late in development. This provides an opportunity to study the neural systems underlying delayed *first* language acquisition, as the neurobiology of language shows a strong degree of biological invariance, with several neural subsystems important in written and spoken language have also been observed when deaf and hearing native signers process American Sign Language (ASL) despite the fact that the eliciting sensory stimuli are very different (Capek, 2004; Capek et al., 2009; MacSweeney, Capek, Campbell, & Woll, 2009). However, it should be noted that although spoken and signed language processing share a number of modality-independent neural substrates, there is also some degree of 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; Capek et al., 2009; MacSweeney et al., 2009; Neville et al., 1998). In support of this hypothesis, we have 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., 2009).

The effects of delayed ASL first language acquisition have been observed in both behavioral and neuroimaging studies. Behavioral studies of deaf individuals with delayed exposure to sign language indicate that with increasing age of acquisition, proficiency in sign language decreases (Mayberry, 1993, 2003; Mayberry & Eichen, 1991; Mayberry, Lock, & Kazmi, 2002). In studies of deaf late-learners of ASL, we have examined the effects of this delayed first language acquisition on brain organization. In one 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, Bavelier, Corina, Jezzard, & Neville, 2002). In a second study, in which we employed ERPs, we 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). All three groups display normal non-cognitive skills. 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.

Using a novel laboratory language-learning task designed to mimic second language immersion, we recently compared the ERP response to novel syntactic rules acquired under conditions of implicit exposure and explicit instruction. Regardless of training condition, learners who successfully acquired the novel syntactic rules showed P600 effects to syntactic violations, similar to those elicited by native speakers that were tested on the same paradigm. This effect was observed after only an hour of exposure to the novel language, demonstrating that late, controlled mechanisms indexed by the P600 can be rapidly recruited (Batterink & Neville, 2013b). In a second study, we examined the neural mechanisms involved in the acquisition of novel semantic information using a task in which novel pseudowords were presented 10 times in a narrative context. During a subsequent explicit recognition task, these novel words elicited a robust N400 effect, suggesting that explicit representations of word meanings can be acquired with remarkable speed (Batterink & Neville, 2011).

We have also examined the role of awareness in semantic and syntactic processing, using attentional blink manipulations. We found that the N400 was elicited only by words that were correctly reported, suggesting that this component indexes processes that are dependent upon awareness (Batterink, Karns, Yamada, & Neville, 2010). Similarly, in the domain of syntactic processing, the P600 was observed only for syntactic violations that were explicitly detected. In contrast, the left anterior negativity (LAN) was elicited by both detected and undetected syntactic violations, suggesting that this response reflects automatic and implicit syntactic processing mechanisms that operate outside of conscious awareness (Batterink & Neville, 2013a).

Several mechanisms may render the neural systems important for syntax and speech segmentation more vulnerable than the neural systems important for semantics. For example, we and others have observed that the neural systems important for syntactic processing show a longer developmental time course than systems important for semantic processing (Hahne, Eckstein, & Friederici, 2004; Sabourin, Pakulak, Paulsen, Fanning, & Neville, 2007), again suggesting that systems with a longer developmental time course may be more modifiable during development. Networks involved in language processing which overlap with networks associated with selective attention may also be more vulnerable. For example, the speech segmentation ERP effect resembles the effect of temporally selective attention (Astheimer & Sanders, 2009), which allows for the preferential processing of information presented at specific time points in rapidly changing streams, has also been shown to modulate early (100 ms) auditory ERPs (Lange & Roder, 2005; Lange, Rosler, & Roder, 2003). 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.

V. Attention

As noted above, many of the changes in vision, audition, sensory integration, and language observed during studies of neuroplasticity may depend at least in part on selective attention. The importance of selective attention for certain types of adult neuroplasticity is 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, 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, 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 utilizing fMRI reveal that selective attention modulates the magnitude and extent of cortical activation in the relevant processing areas (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). Complementary studies using the ERP methodology have clarified the time course of attentional modulation. These studies reveal that in adults, selective attention amplifies the sensori-neural response by 50-100% during the first 100 ms of processing (Hillyard, Di Russo, & Martinez, 2003; Hillyard, Hink, Schwent, & Picton, 1973; Luck, Woodman, & Vogel, 2000; Mangun & Hillyard, 1990). This early attentional modulation is in part domain-general in that it is observed across multiple sensory modalities and is 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 document neuroplasticity in the early neural mechanisms of selective attention that, as in other neural systems, show considerable specificity. In the case of adults born deaf, employing ERPs and fMRI, we observe enhancements of attention that are specific to the peripheral, but not central, visual field (Bavelier et al., 2001; Bavelier et al., 2000; Neville & Lawson, 1987b). In parallel studies of auditory spatial attention among congenitally blind adults, we observe similar specificity in attentional enhancements to peripheral, but not central, auditory locations (Röder, Teder-Sälejärvi, et al., 1999). However, there is some evidence for a sensitive period in attentional changes. For example, adults blinded later in life do not show changes in the early (N1) attention effects, though they do show changes in later (P300) attention effects (Fieger, Röder, Teder-Sälejärvi, Hillyard, & Neville, 2006). Such differences in the specific aspects of attention that are modifiable may also help to explain the apparent lifelong plasticity observed in other types of training in adulthood, including videogaming (e.g., Green & Bavelier, 2003).

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. To address this question, we first developed a child-friendly ERP paradigm for assessing selective auditory attention. These studies were modeled after those we and others have used with adults (Hillyard et al., 1973; Neville & Lawson, 1987a; 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. We presented two different children's stories concurrently from speakers to the left and right of the participant, and then asked participants to attend to one story and ignore the other. We superimposed probe stimuli on the stories and recorded ERPs to these identical probes both when attention was on that story and when it was on the other story. Adults tested with this paradigm show typical N1 attention effects (Coch, Sanders, & Neville, 2005). Children, who show a different ERP morphology to the probe stimuli, also show early attentional

modulation within the first 100 ms of processing. This attentional modulation is an amplification of the broad positivity occurring in this time window, and we observe it in children as young as three years of age (Sanders, Stevens, Coch, & Neville, 2006), see also Figure 3. These data suggest that with sufficient attentional cues, children as young as three years of age can attend selectively to an auditory stream and that doing so, as in adults, alter neural activity within 100 ms of processing. These data provide the baseline from which to examine possible vulnerabilities in children with or at risk for developmental disorders.

In one study, we examined children from different socio-economic status (SES) backgrounds (Stevens, Sanders, & Neville, 2006). Previous behavioral studies indicated that children from lower socioeconomic backgrounds experience difficulty with selective attention, particularly in tasks of executive function and in those tasks that require filtering irrelevant information or suppressing prepotent responses (Farah et al., 2006; Lupien, King, Meaney, & McEwen, 2001; Mezzacappa, 2004; Noble, McCandliss, & Farah, 2007; Noble, Norman, & Farah, 2005). We observed that children from lower SES backgrounds showed reduced effects of selective attention on neural processing (see Figure 3) and, moreover, that these differences were related specifically to a reduced ability to filter irrelevant information (i.e., to suppress the response to ignored sounds). Other research groups report similar results (D'Angiulli, Herdman, Stapells, & Hertzman, 2008). In a second study, we examined children with Specific Language Impairment (SLI) (Stevens et al., 2006). We were interested in children with SLI, as previous behavioral studies reported deficits in aspects of attention including filtering and noise exclusion (Atkinson, 1991; Cherry, 1981; Sperling, Lu, Manis, & Seidenberg, 2005; Ziegler, Pech-Georgel, George, Alanio, & Lorenzi, 2005). We observed that children with SLI did not show effects of selective attention on neural processing, and that this deficit was specific to a reduced ability to enhance the neural response to attended stimuli. 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.

Taken together, these studies point to the two sides of the plasticity in early mechanisms of attention. The marked plasticity observed in attentional systems – and in particular in selective attention – may be mediated by several mechanisms. For example, sustained, selective attention shows a particularly long time course of development. Although the effects of selective attention on neural processing are quite similar in adults and young children, it may be more difficult for children to deploy selective attention successfully. In support of this, a robust literature documents that the abilities to select input for processing and 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; Ridderinkhof & van der Stelt, 2000; Sexton & Geffen, 1979; Zukier & Hagen, 1978). Additionally, since the key sources of selective attention within the parietal and frontal lobes constitute parts of the dorsal pathway, similar neurochemical and anatomical factors noted in the section on vision may contribute to the plasticity of attention. Finally, recent evidence points to considerable genetic effects on attention (Bell et al., 2008; Fan, Fossella, Sommer, Wu, & Posner, 2003; Posner, Rothbart, & Sheese, 2007; Rueda, Rothbart, McCandliss, Saccamanno, & Posner, 2005) that may also be modified by environmental input epigenetically (Bakermans-Kranenberg, Van Ijzendoom, Pijlman, Mesman, & Femmie, 2008; Sheese, Voelker, Rothbart, & Posner, 2007). Thus, a complex interplay of genetic and experiential factors,

operating across a relatively long developmental time course, contribute to the plasticity of selective attention.

VI. Interventions

As described above, selective attention influences early sensory processing across a number of domains. In our most recent research, we are investigating the possibility that attention itself might be trainable, and that this training can impact processing in a number of different domains. We outlined this general argument in a recent review, which applies a cognitive neuroscience framework to identify the role of selective attention in the development of several foundational skills, including language, literacy, and mathematics (Stevens & Bavelier, 2012).

In one line of research, we examined whether training programs that successfully target language or literacy skills also train selective attention. We were interested in this question as several proposals suggest that some interventions designed to improve language skills might also target or train selective attention (Gillam, 1999; Gillam, Crofford, Gale, & Hoffman, 2001; Gillam, Loeb, & Friel-Patti, 2001; Hari, 2001). We tested this hypothesis in a series of intervention studies. In this research, we document changes in the neural mechanisms of selective attention following training in typically developing children, as well as in children with language impairment or at-risk for reading failure (Stevens, Coch, Sanders, & Neville, 2008; Stevens et al., 2013; Yamada, Stevens, Harn, Chard, & Neville, 2011). In all cases, increases in the effects of attention on sensorineural processing are accompanied by behavioral changes in other domains that were also targeted by the training programs, including language and preliteracy skills, and/or changes in the neural systems important for literacy processing. These data suggest that modifications in behavior can arise alongside changes in the early neural mechanisms of attention, and provide a 'proof of concept' for the malleability of the early mechanisms of selective attention in children.

In a second line of research, we have designed training programs that specifically target attention. 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, Thomson, Abbott, & Berninger, 2006; Diamond, Barnett, Thomas, & Munro, 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. However, these previous studies do not engage the larger context of parents and the home environment. Yet the family context plays a key role in supporting children's attention development and may specifically be targeted in intervention programs aimed at improving child outcomes. Thus, employing information from research on the neuroplasticity of selective attention and on the central role of successful parenting in child development, we have now developed and rigorously assessed an eight-week, family-based training program designed to improve brain systems for selective attention in preschool children.

The program, Parents and Children Making Connections – Highlighting Attention (PCMC-A), is unique in combining training sessions for parents / guardians / caregivers (hereafter 'parent') with attention training exercises for children. Parents attend eight weekly, two-hour small-group classes that occur in the evenings or on weekends, and their children

participate in concurrent small group training activities. Parents learn strategies targeting family stress regulation, contingency-based discipline, parental responsiveness and language use, and facilitation of child attention through links to child training exercises. The child component of PCMC-A consists of small-group activities (four-to-six children: two adults) designed to address the fundamental goal of improving regulation of attention and emotion states.

In the evaluation study (Neville et al., 2013), 141 lower SES preschoolers enrolled in a Head Start (HS) program were randomly assigned to the training program, HS-alone, or an active control group. Prior to and following the eight-week intervention period, a multi-rater, multi-method assessment was conducted that included electrophysiological measures of children's selective attention, using the paradigm described above. Results indicated that electrophysiological measures of children's brain functions supporting selective attention, standardized measures of cognition, and parent-reported child behaviors all favored children in the treatment program relative to both control groups. Figure 4 presents the ERP results from this study. Positive changes were also observed in the parents themselves, including changes in language interaction patterns with their children and reductions in parenting stress. Moreover, the effect sizes were large in magnitude, ranging from one-quarter to one-half of a standard deviation.

Importantly, this study both builds on previous research on neuroplasticity and also advances the field in several ways. Perhaps most importantly, the study demonstrates that the neural mechanism of selective attention can be improved in children from lower SES backgrounds, and this can be done in the relatively short timeframe of eight weeks. Second, as the most favorable outcomes were observed in a more parent-focused (as opposed to child-focused) training model, these findings underscore the importance of engaging parents to support child development. Third, the effectiveness of PCMC-A, a short, inexpensive ($800 per family) eight-week program, supports the design of programs that efficiently build on evidence from basic research on neuroplasticity and on evidence-based practices and that can be delivered in relatively short time frames. Finally, by including multiple outcome measures, the study provides a comprehensive picture of the changes resulting from a family-based training model, including not only gains for children in a direct neural measure of selective attention, but also specific skills assessed by standardized tests (Neville, Stevens, Klein, Fanning, Bell, Cakir, et al., 2011; Neville, Stevens, Klein, Fanning, Bell, Isbell, et al., 2011; Neville et al., 2013).

VII. Conclusions

The research described in this chapter illustrates 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 highlights 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 now entering a powerful frontier of neuroplasticity research that transforms the results of basic research on the profiles and mechanisms of neuroplasticity into 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.

Acknowledgements

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Figure 1. Performance on a peripheral visual field motion detection 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. Deaf participants showed enhancements and dyslexic participants showed deficits relative to matched controls. No differences between groups were observed on a central visual field contrast sensitivity task. Data from Stevens & Neville (2006).
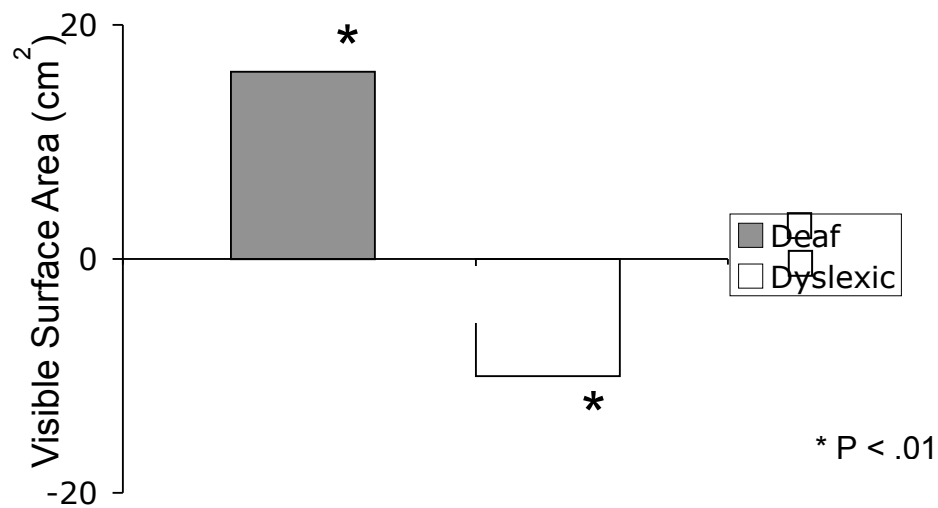
Figure 2. Event-related brain potential (ERP) to syntactic violations in spoken sentences showing independent effects of age of acquisition and proficiency on neural processing for language. (a) Comparison of high-proficiency second-language learners to native speakers, of equivalent proficiency, and (b) Comparison of native speakers with higher versus lower levels of English language proficiency. Data from Pakulak & Neville 2010 and Pakulak & Neville 2011.
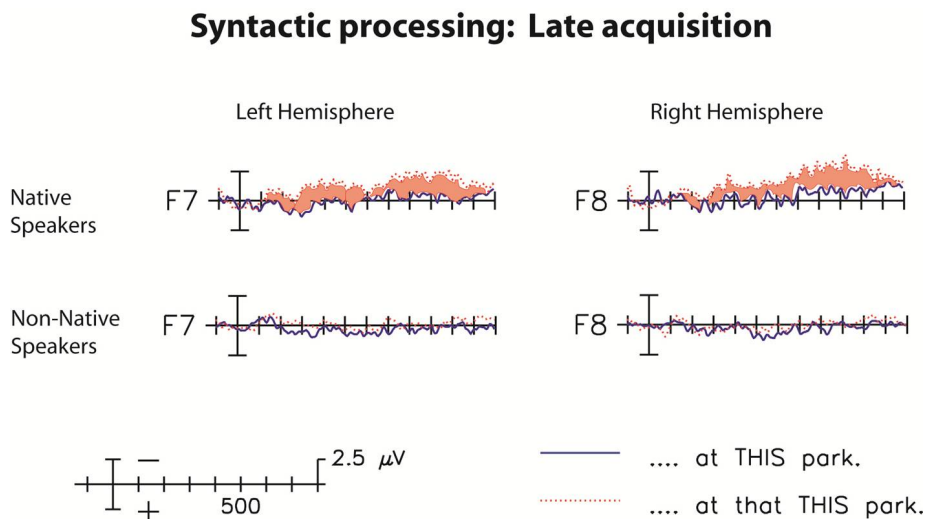
(a)
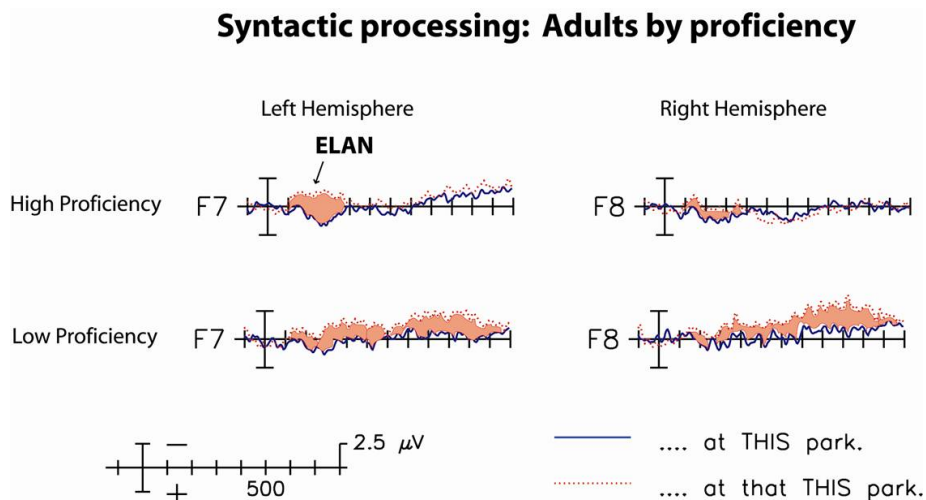
(b)

Figure 3. Effects of selective attention on neural processing in children aged 3-8 years from higher versus lower socioeconomic status (SES) backgrounds. Children from higher SES backgrounds had significantly greater effects of selective attention on neural processing than children from lower SES backgrounds. Data from Stevens, Lauinger, & Neville, 2009.
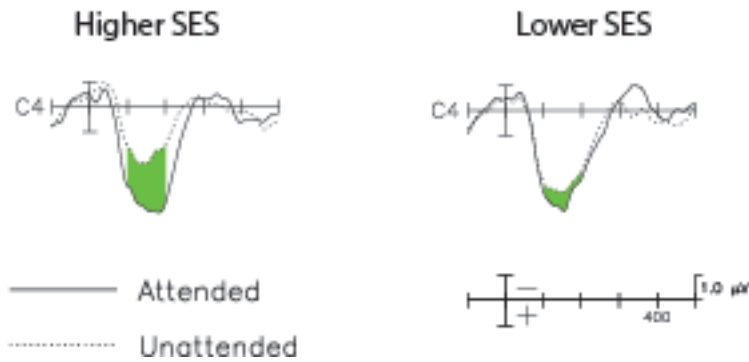
Figure 4. Effects of selective attention on neural processing in children aged 3-5 years from lower socioeconomic status backgrounds, both before and after an 8-week training period. Only children in the family-based program with a greater emphasis on parent training ("PCMC-A") showed an increase in the effects of attention on neural processing. Children in Head Start – Alone (HS-Alone) or in a comparison training program ("ABC") did not show significant changes in the effects of attention on neural processing from pre- to post-training. Children in the PCMC-A program also made significantly greater gains than either comparison group on standardized measures of receptive language and nonverbal IQ, as well as parent reports of child behavior. See main text for details. Data from Neville, Stevens, Pakulak, Bell, Fanning, Klein, & Isbell, 2013.