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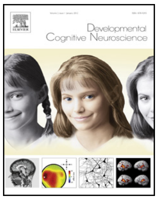

Auditory attention in childhood and adolescence: An event-related potential study of spatial selective attention to one of two simultaneous stories

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A B S T R A C T

Auditory selective attention is a critical skill for goal-directed behavior, especially where noisy distractions may impede focusing attention. To better understand the developmental trajectory of auditory spatial selective attention in an acoustically complex environment, in the current study we measured auditory event-related potentials (ERPs) across five age groups: 3–5 years; 10 years; 13 years; 16 years; and young adults. Using a naturalistic dichotic listening paradigm, we characterized the ERP morphology for nonlinguistic and linguistic auditory probes embedded in attended and unattended stories. We documented robust maturational changes in auditory evoked potentials that were specific to the types of probes. Furthermore, we found a remarkable interplay between age and attention-modulation of auditory evoked potentials in terms of morphology and latency from the early years of childhood through young adulthood. The results are consistent with the view that attention can operate across age groups by modulating the amplitude of maturing auditory early-latency evoked potentials or by invoking later endogenous attention processes. Development of these processes is not uniform for probes with different acoustic properties within our acoustically dense speech-based dichotic listening task. In light of the developmental differences we demonstrate, researchers conducting future attention studies of children and adolescents should be wary of combining analyses across diverse ages.

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1. Introduction

Selective attention, the ability to enhance the processing of certain stimuli while suppressing the information from other concurrent stimuli, is critical for regulating external sensory input and occurs within and across sensory modalities (e.g. visual: Çukur et al., 2013, somatosensory: Forster et al., 2009, intermodal: Karns and Knight, 2009, and auditory: Woods et al., 2009). This cognitive ability is fundamental for academic success (Blair and Razza, 2007; Rueda et al., 2010; reviewed in Stevens and Bavelier, 2012). Auditory attention in particular is highly relevant to a school setting in which instruction and completion of assignments may occur in an acoustically noisy environment with competing speech streams. Additionally, the enhancement and suppression of sensory stimulation are disrupted in many children with developmental disorders, including individuals with autism (Reinvall et al., 2013), attention-deficit disorder (Gomes et al., 2013), at-risk readers (Stevens et al., 2013), dyslexia (Johnson et al., 2013; Stefanics et al., 2011), language impairment (Stevens et al., 2008), deafness (Dye and Hauser, 2013), and non-disordered special populations such as children of lower socioeconomic status (D’Angiulli et al., 2008; Stevens et al., 2009). Selective attention is also key to general processes of neuroplasticity (Neville and Lawson, 1987; Röder et al., 1999; Stevens and Neville, 2006) and understanding the typical developmental trajectory of attention is critical to establish and evaluate the immediate and long-term outcomes of attention-training interventions for children and adolescents (Diamond and Lee, 2011; Neville et al., 2013; Shonkoff, 2011).

The neural indices of selective auditory attention have been extensively studied in adults using dichotic listening paradigms (for a review, see Hopfinger et al., 2004). In adults, event-related potential (ERP) studies with dichotic listening paradigms indicate that spatial auditory selective attention typically modulates the amplitude of neural response to an attended stimulus at the N1 latency (Hillyard et al., 1973; Hillyard, 1981), an increase that could also reflect changes to signal to noise such as increased temporal consistency (Thornton et al., 2007). Attention modulation can also have scalp topographies that are distinct from the sensory

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ERP responses; these are thought to index additional endogenous processing of attended stimuli (Hansen and Hillyard, 1980). Attention modulation can occur as early as 50 ms under certain experimental conditions (Giuliano et al., 2014; Woldorff et al., 1987; Woldorff and Hillyard, 1991) and with intermodal selective attention (Karns and Knight, 2009). This early-latency modulation is consistent with primary cortical processing (Deiber et al., 1988; Liégeois-Chauvel et al., 1994; Woods et al., 1995) and scalp topographies and source modeling of early-latency attention modulations are consistent with sources in the temporal auditory cortices (Weisser et al., 2001; Woldorff et al., 1993). This modification of early sensory processing likely relies upon slowly-developing substrates of distributed cortical attention networks such as the frontal cortex (Knight et al., 1989). One way to view early latency amplitude modulation of ERPs is that the frontal cortex and other brain systems supporting attention hold sensory cortex in a state that is more receptive to processing the attended stimuli than unattended (Karns and Knight, 2009).

ERP studies have demonstrated that the ability to direct auditory spatial attention is evident in the early years of childhood at adult-like latencies of 100 ms (Coch et al., 2005; Sanders et al., 2006) but studies in other domains highlight the limits of child attention. Behavioral studies using dichotic listening tasks have indicated that children have less effective selection abilities (Geffen and Sexton, 1978; Hiscock and Kinsbourne, 1980; Takio et al., 2009) and ERP studies using target-detection paradigms have indicated that both 9- and 12-year-olds show latency, amplitude, and behavioral differences relative to adults (Gomes et al., 2007). Similarly, in a dichotic listening task that required attending to either specific pitch ranges or syllables to detect deviant targets, developmental differences in the neurophysiology of selective attention were observed between children, young adolescents, and adults, but only after 200 ms (Berman and Friedman, 1995). Likewise, in an auditory oddball paradigm with 9–12 year-old children, younger adults, and older adults, age-related differences were reported for the peak latency, peak amplitude, and scalp distribution of components related to selective auditory attention (Mueller et al., 2008). In older children (ages 9–12) there is also evidence that task-relevance shapes complex auditory scene analysis (Sussman and Steinschneider, 2009) but unfortunately the requirement of an overt response by participants limits the age-range for such tasks to older children. In very young children, engaging tasks that manipulate attention without an overt response are particularly important and also allow comparison to older age groups.

Although we have successfully used our naturalistic story-based dichotic listening task to record ERP markers of selective auditory attention in typically-developing children (Coch et al., 2005; Sanders et al., 2006), in clinical and at-risk populations (Stevens et al., 2006, 2008, 2012, 2013), and in children of lower socioeconomic status (Neville et al., 2013; Stevens et al., 2009, 2014), these previous studies did not include adolescents, and there is ample evidence indicating that systems that support attention, such as the frontal and parietal cortices, continue to mature throughout early adolescence (e.g. Berman and Friedman, 1995; Gomes et al., 2007; Mueller et al., 2008; for a review see Segalowitz et al., 2010). To our knowledge, there has been little work that included older adolescents as a potentially distinct age group, and tracked the development of auditory attention from early childhood into adulthood using the same ERP task. Because of the slower developmental timescale of the frontal-parietal attention network (Yurgelun-Todd, 2007) it is highly likely that spatial attentional selection also continues to mature in this older age range.

In studies of children and adolescents across a broad age range, it is important to interpret developmental changes in attention in the context of the continuing development of the auditory system and frontal cortex. While the auditory brainstem forms early and is myelinated by 37 weeks gestation (Eggermont, 1988) most synapses in the cerebral cortex form after birth, occurring concurrently with growth of dendrites and axons, and myelination of subcortical white matter. Synaptic density peaks in infancy and early childhood followed by pruning through late childhood and adolescence. This occurs on different timescales in the auditory and frontal cortices. In the auditory cortex, synaptic density is maximal at 3 months of age in contrast to 15 months for frontal cortex. Synapse elimination is complete by 12 years of age for the auditory cortex, but continues into mid-adolescence for frontal cortex (Huttenlocher and Dabholkar, 1997) highlighting the non-uniform nature of cortical development in different brain systems.

Given the dynamic process of synaptic growth and pruning occurring across development, it is not surprising that there are striking developmental changes in the morphology of the auditory evoked potentials, which reflect inhibitory and excitatory post-synaptic electrical potentials, from childhood to adulthood. In particular, the P1–N1 complex shows a prolonged developmental time course (Ponton et al., 2000), with the N1 developing later and maturing more slowly than the P1, and a reduction of age-related changes in the later latency P2 and N2 components (Ponton et al., 2002). Despite maturational changes in auditory evoked potentials observed at the scalp, dipole source modeling suggests that the orientations of the generators for the P1–N1–P2–N2 complex are adult-like by 5 years of age (Ponton et al., 2002). In a dichotic listening task with simultaneous stories presented with the story on one side attended, the typical adult response to a brief auditory probe is a P1–N1–P2 complex at the same latency – or for linguistic probes a P1 followed by a later N1. Meanwhile, for young children (3–8 years old) auditory evoked potentials consist of a broad initial positivity from 100 to 300 ms that is modulated by attention (Coch et al., 2005; Sanders et al., 2006). While a negative-going attention modulation at the N1 is the prototypical spatial attention effect in adults (i.e., Hink and Hillyard, 1976), we have recently shown that attention can instead modulate the adult P1 in a linguistic dichotic listening task (Giuliano et al., 2014). Previous researchers have noted that the ability to select among competing stimuli, enhancing the processing of the task-relevant information, is available in very young children, but that the processing speed and efficiency may be what improves as children develop (Ridderinkhof and van der Stelt, 2000) so this very early P1 mechanism of attention modulation might not yet be available to younger children or adolescents.

We undertook the present study to determine how auditory selective attention changes across childhood and adolescence. At first glance, a positive attention effect in young children and a negative attention effect in adults might be construed as a possible polarity reversal of an attention related component superimposed on the auditory evoked potentials. However, an alternative explanation is an attention process that operates as a gain-control mechanism of the auditory evoked potentials, changing the amplitude of the developing auditory evoked potentials such as the P1 and N1. The latency at which this mechanism can operate may develop over the course of childhood and adolescence as underlying cortical systems mature. Our hypothesis in light of previous studies (Sanders et al., 2006; Coch et al., 2005) was that attention modulation at early-latencies, from childhood through adolescence, is best understood as a gain-control modulation of maturing auditory evoked potentials. Furthermore, additional sustained and likely endogenous attention-related processes that are typically deployed at later latencies may also be engaged differentially as neural systems mature. We anticipated, based on previous work with 6–8 year olds that additional sustained processes may distinguish different age groups at later latencies in the 300–450 ms time range (Coch et al., 2005; Sanders et al., 2006). We used a naturalistic dichotic listening task with simultaneously presented

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