

Auditory and visual refractory period effects in children and adults: An ERP study

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Abstract

Objective: This developmental study was designed to investigate event-related potential (ERP) refractory period effects in the auditory and visual modalities in children and adults and to correlate these electrophysiological measures with standard behavioral measures.

Methods: ERPs, accuracy, and reaction time were recorded as school-age children and adults monitored a stream of repetitive standard stimuli and detected occasional targets. Standards were presented at various interstimulus intervals (ISIs) in order to measure refractory period effects on early sensory components.

Results: As has been reported previously in adults, larger components for standards with longer ISIs were observed for an auditory N1 and the visual occipital P1 and P2 in adults. Remarkably similar effects were observed in children. However, only children showed refractory effects on the amplitude of the visual N1 and P2 measured at anterior sites. Across groups, behavioral accuracy and reaction time were correlated with latencies of auditory N1 and visual P2 across ISI conditions.

Conclusions: The results establish a normal course of development for auditory and visual ERP refractory period effects across the 6- to 8-year-old age range and indicate similar refractoriness in the neural systems indexed by ERPs in these paradigms in typically developing children and adults. Further, the results suggest that electrophysiological measures and standard behavioral measures may at least in part index similar processing in the present paradigms.

Significance: These findings provide a foundation for further investigation into atypical development, particularly in those populations for which processing time deficits have been implicated such as children with specific language impairment or dyslexia.

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1. Introduction

Numerous behavioral, psychometric studies of auditory and visual system development in school-age children have clearly shown that aspects of sensory processing continue to develop across childhood into adolescence (e.g., Allen et al., 1989; Buckingham and Kelly, 1996; Fior, 1972; Hollants-Gilhuijs et al., 1998a,b; Kovács et al., 1999; Lenihan et al., 1971; Maxon and Hochberg, 1982). In consonance, anatomical and MRI data indicate that both the extrastriate

and auditory cortices continue to develop at least until adolescence (e.g., see Garey, 1984; Huttenlocher and Dabholkar, 1997; Moore and Guan, 2001; Sowell et al., 1999; Thompson et al., 2000; Yakovlev and Lecours, 1967). However, relatively little is known about the on-line functional development of basic auditory and visual processing across the school-age years, in part due to the paucity of adequate methodologies useable with children.

The recording of event-related potentials (ERPs) is one non-invasive functional imaging method with exquisite temporal resolution that is amenable to use with children. ERPs are voltage fluctuations in the ongoing electroencephalogram (EEG) in response to controlled stimulus presentations, and have proven sensitive to the cortical activation patterns underlying sensory and perceptual processes

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(e.g., see Rugg and Coles, 1995). Scalp-recorded ERPs reflect the stimulus-locked information processing activities, in terms of net electrical fields, of large assemblies of neurons in different areas of the brain on a timescale of milliseconds (e.g., see Coles and Rugg, 1995). The individual components that constitute the ERP waveform index particular types of information processing, with the early components reflecting activity within sensory systems.

A number of ERP studies have investigated the development of auditory and visual sensory systems and many of the early components of the ERP waveform have been shown to change over time. For example, in the auditory modality, peak latencies of P1, N1, and N2 have been shown to decrease with increasing age from childhood to late adolescence (Borg et al., 1988; Enoki et al., 1993; Fuchigami et al., 1993; Goodin et al., 1978; Oades et al., 1997; Paetau et al., 1995; Rojas et al., 1998; Tonquist-Uhlén et al., 1995). In the visual modality, researchers have similarly reported (non-monotonic) decreases in amplitude of occipital responses to visual stimuli with increasing age (Barnet et al., 1980; Breclj et al., 2002; Buchsbaum et al., 1974; Callaway and Halliday, 1973; Dustman and Beck, 1969), with waveforms to some stimuli still not adult-like at the age of 5 years (Blom et al., 1980; Moscovitz and Sokol, 1983; Sokol and Jones, 1979). Much of the developmental research in the visual modality focuses on infancy rather than childhood (e.g., see Eggermont, 1988).

Recently, there have been a number of reports further investigating the development of the auditory evoked potential, with results confirming and extending earlier findings of change in AEP components into adolescence (e.g., Albrecht et al., 2000; Bruneau et al., 1997; Ponton et al., 2000, 2002). (To our knowledge, no similar recent research has been conducted within the visual domain.) For example, Bruneau et al. (1997) reported differential topography of the N1 in adults (frontocentral maximum) and children (midtemporal maximum), while Ponton et al. (2000) reported gradual latency decreases in P1 and N1(b) and increasing latency in N2 with more step-like amplitude changes from age 5 to 20, dependent on recording location. Further, it appears that maturation rates are not the same throughout the auditory system, such that P2 matures earlier in comparison to N1(b) (Ponton et al., 2000). Dipole source modeling has suggested that the generators contributing to these components may indeed mature at different rates, with, for example, maturation of the generators of the auditory N1(b) and P1 relatively slow in comparison to those for N2 (Ponton et al., 2002; see also Albrecht et al., 2000). It has been suggested (Ponton et al., 2002) that this extended development may be related to the prolonged development of superficial layers of the human auditory cortex (e.g., Moore and Guan, 2001).

Across developmental studies of the auditory evoked potential, there is some controversy regarding waveform morphology. While adult waveforms typically evidence a P50/P1 followed by an N1, children's waveforms

sometimes show a large P1 followed by a negativity at 200–250 ms (termed N1b in some reports and N250 in others, e.g., Albrecht et al., 2000; Bruneau et al., 1997; Ceponiene et al., 1998; Courchesne, 1990; Korpilahti and Lang, 1994; Kurtzberg et al., 1995; Paetau et al., 1995; Ponton et al., 2000; Sharma et al., 1997). The relationship between the child N1b/N250 and the adult N1 is unknown, with some authors suggesting homology (e.g., Korpilahti and Lang, 1994; Kurtzberg et al., 1995) and others claiming two distinct components (e.g., Csépe, 1995; Ponton et al., 2002; Takeshita et al., 2002). Reports of different topography for the first negative peaks in the auditory waveforms of young children and adults (e.g., Bruneau et al., 1997) support the claims of distinct components and indexed neural systems, as do reports of different component structure based on dipole analyses (e.g., Albrecht et al., 2000; Ponton et al., 2002; Takeshita et al., 2002).

Notwithstanding these accumulating findings regarding the normal course of maturation of the human auditory system in terms of ERPs, there is still much to be learned about basic sensory functional development; in particular, little is known about the refractory properties of developing sensory neural networks. It has been shown that ERPs can be used to assess relative refractory periods or recovery cycles for aspects of the auditory and visual systems in paradigms in which a stimulus is presented repeatedly at different interstimulus intervals (ISIs) or pairs of stimuli are presented at different ISIs. In adults, the amplitude of early (100–200 ms) modality-specific ERP components is reduced as stimulus repetition rate is increased. This decrease in responsiveness with decrease in ISI is thought to be a reflection of the lack of excitability of the population of responding cortical neurons, and an index of processing rates within cortical sensory areas (Gastaut et al., 1951). Thus, theoretically, an increase in ERP amplitude to the same stimulus presented with a longer ISI as compared to a shorter ISI is a reflection of the greater physiological recovery over time of the neurons generating the response to that stimulus. It is likely that different populations of neurons have different recovery cycles and that refractoriness of these different networks may have different developmental time courses.

The refractory rate of neuronal populations has been studied in cats and monkeys as well as in humans (e.g., Chang, 1951; Demetrescu and Steriade, 1967; Neville and Foote, 1984; Rosenzweig and Rosenblith, 1950). In the visual modality, studies with adult humans using stimuli with relatively short ISIs have suggested that the recovery cycle extends beyond 200 ms (Bergamasco, 1966; Cigánek, 1964; Floris et al., 1967; Galvin et al., 1976; Musselwhite and Jeffreys, 1983; Riemslog et al., 1985; Skrandies and Raile, 1989). Studies using stimuli with longer ISIs have confirmed a lengthy visual recovery cycle for component amplitude extending beyond 6 s (Lehtonen, 1973). MEG response recovery studies have suggested that occipital

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