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Research paper

Theta, beta and gamma rate modulations in the developing auditory system

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ABSTRACT

In the brain, the temporal analysis of many important auditory features relies on the synchronized firing of neurons to the auditory input rhythm. These so-called neural oscillations play a crucial role in sensory and cognitive processing and deviances in oscillatory activity have shown to be associated with neurodevelopmental disorders. Given the importance of neural auditory oscillations in normal and impaired sensory and cognitive functioning, there has been growing interest in their developmental trajectory from early childhood on.

In the present study, neural auditory processing was investigated in typically developing young children ($n = 40$) and adults ($n = 27$). In all participants, auditory evoked theta, beta and gamma responses were recorded. The results of this study show maturational differences between children and adults in neural auditory processing at cortical as well as at brainstem level. Neural background noise at cortical level was shown to be higher in children compared to adults. In addition, higher theta response amplitudes were measured in children compared to adults. For beta and gamma rate modulations, different processing asymmetry patterns were observed between both age groups. The mean response phase was also shown to differ significantly between children and adults for all rates.

Results suggest that cortical auditory processing of beta develops from a general processing pattern into a more specialized asymmetric processing preference over age. Moreover, the results indicate an enhancement of bilateral representation of monaural sound input at brainstem with age. A dissimilar efficiency of auditory signal transmission from brainstem to cortex along the auditory pathway between children and adults is suggested. These developmental differences might be due to both functional experience-dependent as well as anatomical changes. The findings of the present study offer important information about maturational differences between children and adults for responses to theta, beta and gamma rates. The current study can have important implications for the understanding of developmental disorders which are known to be associated with deviances in neural auditory processing.

1. Introduction

The neural processing of important temporal auditory features is established by neural oscillatory activity that fires synchronously to the rhythm of the input signal (Luo and Poeppel, 2007). This process is thought to involve the creation of additive neural-population responses next to the ongoing spontaneous neural oscillations, resulting in stimulus-evoked neural oscillations (Shah et al., 2004). Neurons in the brain fire synchronously to the auditory rhythm across a wide range of stimulus modulation frequencies (Zaehle et al., 2010). In general, response amplitudes decrease with increasing modulation rate (Picton, 2011). However, from delta (<4 Hz) to gamma (>30 Hz) rates regions of increased response peaks occur in the neural temporal modulation transfer function, including for stimulus rates near 4, 10, 20, 40 and 80 Hz (Alaerts et al., 2009; Picton, 2011). Responses to amplitude modulations below 50 Hz in particular offer important information, as they characterize the rates of the temporal envelope of speech (Edwards and Chang, 2013; Füllgrabe et al., 2009). Within this

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temporal envelope, responses to rates near 4 and 20 Hz are of specific importance as they correspond to rates by which syllables and phonemes respectively appear in speech (Rosen, 1992). Indeed, there is a remarkable correspondence between the average duration of phonemes (20–50 ms) and syllables (250 ms) in speech on the one hand and beta (15–30 Hz) and theta (4–8 Hz) ranges on the other hand (Ghitza, 2011). Speech perception theories suggest that the left and right hemisphere have a functional preference to process certain ranges of stimulus modulations rates (Boemio et al., 2005; Obrig et al., 2010). In that respect, the multi-time resolution theory in particular raised recently attention in literature (Poeppel, 2003). This theory proposes that the information at different temporal rates is encoded by the stimulus-induced synchronization of cortical rhythms at two time scales. Responses to low rates would be dominantly processed in the right hemisphere whereas responses to high rates would be dominantly processed in the left hemisphere or bilateral (Poeppel et al., 2008).

Auditory oscillations have mostly been studied in humans using electroencephalography (EEG). EEG records the summed effect of the synchronous postsynaptic activity in a large number of neurons (Rance, 2008). Several studies have demonstrated the importance of auditory oscillations for sensory and cognitive abilities (e.g. Thut et al., 2012; Gross et al., 2013). Deviances in neural oscillatory activity, such as reduced cerebral lateralization, have been shown to be associated with neurodevelopmental disorders (Bishop, 2013). More specifically, atypical lateralization patterns have been found in individuals with language and literacy impairments such as developmental dyslexia and specific language impairment (De Guibert et al., 2011; Goswami, 2011). In these disorders, a lack of lateralization or an atypical hemispheric processing asymmetry was observed at auditory stimulus rates of interest to speech and language processing such as phonemes (beta) and syllables (theta) (e.g. Abrams et al., 2009; Lehongre et al., 2011). Other studies showed specific processing deviances in individuals with language and literacy problems in the processing of higher oscillatory rates such as gamma rates (Heim et al., 2013; Hornickel et al., 2009). In addition, atypical cerebral lateralization has also been linked to cognitive dysfunction and disorders such as schizophrenia (Edgar et al., 2006; Groen et al., 2012).

In normal development, the responses to modulation rates are altered over the course of maturation by anatomical and maturational changes. The maturational period of responses to higher rates is known to be shorter than the maturational period of lower rates. While responses in the frequency domain of 4, 20 and 40 Hz have been demonstrated to significantly differ between children and adults, responses to 80 Hz have been thought to change little with age (Pethe et al., 2004; Tlumak et al., 2012). However, a recent study showed that the maturational period for such higher rates would be more prolonged than initially assumed (Skoe et al., 2013). Lower and higher stimulus modulation rates are processed by different neural structures. In general, the lower the stimulus modulation frequency, the higher in the auditory pathway the response generator (Herdman et al., 2002; Picton, 2011). Amplitude modulations below 32 Hz are found to be dominantly processed by cortical structures. Hereby, the lowest rates corresponding to the syllable rate (4–8 Hz) are processed in the secondary auditory cortex, while the primary auditory cortex is sensitive to modulations rates up to 32 Hz (Liégeois-Chauvel et al., 2004). Subcortical activation is found for amplitude modulations ranging from 32 to 256 Hz in the superior olivary complex and the inferior colliculus (Giraud et al., 2000).

In general, auditory evoked response asymmetries are known to increase with maturity from infancy to adulthood (Minagawa-Kawai et al., 2011; Wunderlich et al., 2006) and decrease again in the elderly brain (Cabeza, 2002). However, very little is known about the development of functional auditory asymmetry in early childhood. More specifically, information about the critical period in child development around the onset of reading acquisition is lacking. Investigating five-year-olds attending the last year of kindergarten could offer important information as this population is about to undergo important changes in their language and literacy network by the acquisition of reading. Indeed, a recent study indicated that, although continued maturational plasticity occurs until young adulthood, substantial differences in auditory processing arise from the age of five years on (Skoe et al., 2013). A better view on typical maturational differences between prereading five-year-olds and mature adult readers could improve our understanding of the neurodevelopmental basis of auditory processing. This in turn might help to identify the association between atypical lateralization and neurodevelopmental disorders and to detect atypical auditory development in the framework of cognitive, language and literacy disorders.

The present study aims to examine the maturational differences between young children and adults in auditory response characteristics to theta, beta and gamma rate modulations and distinguishes between the recorded response amplitude and neural background noise. In addition, this study aims to explore the maturational differences in response asymmetries and phase along the auditory pathway in a typical developing population. To investigate this, auditory steady-state responses (ASSR) to rates in the theta, beta and gamma range were recorded in typically developing five-year-old children and young adults. We focused on stimulus rates within the oscillatory ranges that occur on time scales particularly important for speech perception. Response amplitudes and neural background noise were analyzed as a function of participant age (children versus adults), stimulus type (cortical versus brainstem rates) and hemispheric recording side (left versus right). This study is unique in that it compares several important neural auditory processing parameters such as hemispheric processing preference, response strength, neural background noise and phase coherence at cortical and brainstem level in a well-defined group of young children and adults with a narrow age-range. Outcomes will provide information regarding normal auditory maturational differences and response asymmetries between five-year-olds and mature young adults, and might be useful for the investigation of both typical and deviant auditory development.

2. Material and methods

2.1. Participants

In this study, 40 young children (age: 62 months ± 3 months; 16 female) and 27 young adults (age: 21 years ± 3 years, 22 female) participated. The children were recruited from a large longitudinal study (Vanvooren et al., 2014). Adults were recruited from a population of students. All participants were native Dutch speakers, without a history of brain damage, language problems, visual problems or hearing loss. Additionally, participants were required to have adequate nonverbal intelligence, defined by an IQ score above 85 on the Raven Coloured Progressive Matrices (Raven et al., 1984) and to be right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Furthermore, they had to have normal audiometric pure-tone hearing thresholds (i.e., 20 dB HL or less for all octave frequencies from 0.5 to 4 kHz) and an unremarkable otoscopic and tympanometric examination.