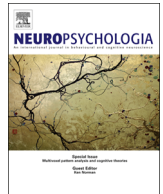




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Oscillatory support for rapid frequency change processing in infants

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ABSTRACT

Rapid auditory processing and auditory change detection abilities are crucial aspects of speech and language development, particularly in the first year of life. Animal models and adult studies suggest that oscillatory synchrony, and in particular low-frequency oscillations play key roles in this process. We hypothesize that infant perception of rapid pitch and timing changes is mediated, at least in part, by oscillatory mechanisms. Using event-related potentials (ERPs), source localization and time-frequency analysis of event-related oscillations (EROs), we examined the neural substrates of rapid auditory processing in 4-month-olds. During a standard oddball paradigm, infants listened to tone pairs with invariant standard (STD, 800–800 Hz) and variant deviant (DEV, 800–1200 Hz) pitch. STD and DEV tone pairs were first presented in a block with a short inter-stimulus interval (ISI) (Rapid Rate: 70 ms ISI), followed by a block of stimuli with a longer ISI (Control Rate: 300 ms ISI). Results showed greater ERP peak amplitude in response to the DEV tone in both conditions and later and larger peaks during Rapid Rate presentation, compared to the Control condition. Sources of neural activity, localized to right and left auditory regions, showed larger and faster activation in the right hemisphere for both rate conditions. Time-frequency analysis of the source activity revealed clusters of theta band enhancement to the DEV tone in right auditory cortex for both conditions. Left auditory activity was enhanced only during Rapid Rate presentation. These data suggest that local low-frequency oscillatory synchrony underlies rapid processing and can robustly index auditory perception in young infants. Furthermore, left hemisphere recruitment during rapid frequency change discrimination suggests a difference in the spectral and temporal resolution of right and left hemispheres at a very young age.

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1. Introduction

The ability to process and categorize rapidly changing acoustic signals is a critical component of language acquisition and communication. Similar words can have very different meanings based on acoustic differences over tens of milliseconds. The words “dog” and “bog”, for example, have very different meanings and associations, yet differ acoustically over only the first 40 ms. The perception and mapping of these differences emerges in the process of language acquisition. For example, perception of phonetic boundaries based on small acoustic differences can emerge in infants as

young as 2 months old (Aslin, 1989; Eilers, Morse, Gavin, & Oller, 1981; Irwin, Ball, Kay, Stillman, & Rosser, 1985; Jusczyk, Pisoni, Walley, & Murray, 1980), but the response to or use of these acoustic-phonetic categories comes much later in development. It is thought that deficits in the ability to perceive rapidly changing acoustic differences are either a cause [(Tallal, Merzenich, Miller, & Jenkins, 1998) for review] or a consequence (Bishop, Hardiman, & Barry, 2012; Bishop et al., 1999) of language impairments, affecting not only speech understanding, but also language comprehension and reading ability.

Converging evidence strongly suggests that the ability to process rapid changes in acoustic frequency and timing has a neurophysiological basis. Specifically, longitudinal and cross-sectional studies combining electroencephalography (EEG), event-related potentials (ERPs) and perceptual measures have shown strong, predictive correlations between basic acoustic processing discrimination in infants and later language outcomes (Benasich, Thomas, Choudhury, & Leppanen, 2002; Choudhury, Leppanen, Leevers, & Benasich, 2007; Hamalainen, Salminen, & Leppanen, 2012). These studies show that the robustness of ERP responses to tones in the first year of life can predict language

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ability at 3, 4 and 5 years of age. These problems may persist, as neural transcription of the rapid changes in speech sounds has been shown to be disrupted in school-aged children with language and learning problems (Banai, Nicol, Zecker, & Kraus, 2005; Hornickel, Anderson, Skoe, Yi, & Kraus, 2012; Russo, Nicol, Musacchia, & Kraus, 2004; Wible, Nicol, & Kraus, 2004) and is sensitive to learning effects well into adulthood (Musacchia, Strait, & Kraus, 2008; Musacchia, Sams, Skoe, & Kraus, 2007; Skoe & Kraus, 2012; Wong, Skoe, Russo, Dees, & Kraus, 2007).

In ERP studies of rapid auditory processing with children and adults, two main stimulus factors are often considered: rate (which can be related to differences in phonetic Voice Onset Time) and frequency change over time (e.g. spectral changes in formant transitions). Both adults and school-aged children have shown consistent changes in the morphology of ERP waveforms as a function of decreasing presentation rate [for review see, (Crowley & Colrain, 2004; Naatanen & Picton, 1987)]. In adult studies with single tones, ERP peak amplitude has been shown to decrease with decreased inter-stimulus intervals (ISI) of < 100–200 ms (He, Hotson, & Trainor, 2009; Naatanen, 1992; Ponton, Eggermont, Kwong, & Don, 2000). Age and maturation have a profound impact on rate-related effects at specific ERP peaks, which suggest a developmental trajectory of temporal resolution. For example, in adults, the P₁–N₁–P₂–N₂ complex is suppressed as stimulus rate increases from 400 to 800 ms ISI and the P₁–N₁ complex is “merged” into a single peak with a latency between P₁ and N₁ (Sussman, Steinschneider, Gumenyuk, Grushko, & Lawson, 2008). In the same study, children between 8 and 11 years of age were shown to, have an immature, P₁ bifurcated peak at slower rates which further fused into a broad positivity at faster rates. A merged response with short tone-pair ISIs has also been observed in infants; however, rapid presentation with these stimuli is associated with an increase in peak amplitude (Choudhury & Benasich, 2011). Taken together, these data suggest that the functional brain response to rapidly changing acoustics varies as a function of age and rate of presentation.

Pertaining to rapid frequency discrimination, ERP differences have been observed in response to rapid frequency change of tones (e.g. 100–300 Hz at 70 ms ISI) between groups of typically developing infants and those at-risk for developing language impairments via their family history (Choudhury & Benasich, 2011). These data suggest that, as a group, infants with a family history of language disorders may have poorer spectrotemporal resolution of acoustic change as early as 6 months-of-age. When the groups were combined, both normal and at-risk infants showed a strong correlation between the brain response to rapid frequency change at 6 months-of-age and language outcomes at 3 and 4 years-of-age. Despite previous evidence supporting the role of rapid auditory processing skills in auditory and language development, questions about the neuronal mechanisms that underlie efficient rapid processing remain. This is of interest to further understanding of the neurophysiology of typical auditory function in development, as well as allowing better insight into the ontogeny of developmental language disorders and communication shortfalls that have been characterized by auditory processing deficits.

Several lines of evidence suggest that neuronal oscillations may play a crucial mechanistic role in the development of rapid auditory processing. Neuronal oscillations are periodic fluctuations in the activity of a single neuron (Llinas & Yarom, 1986) or ensemble of neurons (Bishop, 1933), that reflect cyclic shifts in excitability an active neuronal population (Buzsaki, 2002) and control the excitatory response of said population [(Lakatos, Pincze, Fu, Javitt, Karmos, & Schroeder, 2005) for review, see (Buzsaki, 2006; Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008)]. In general, auditory processing relies on a highly complex

network of cortical and sub-cortical auditory nuclei (Kaas & Hackett, 2000), a great degree of brain specialization for specific sounds and sound combinations (Kaas, Hackett, & Tramo, 1999; Rauschecker, Tian, & Hauser, 1995; Tian, Kusmierck, & Rauschecker, 2013) and, as with multiple cortical and subcortical networks, coordinated and synchronized oscillatory activity within and across local populations (Buzsaki, 2004; Buzsaki & Draguhn, 2004; Destexhe, Contreras, & Steriade, 1998; Lakatos, Chen, O’Connell, Mills, & Schroeder, 2007; Lakatos et al., 2005). As brain development proceeds, oscillatory coupling at a neuron’s synapse increases from uncorrelated, transient electrical transmission to synchronous periodic patterns in several frequency bands (Ben-Ari, 2001) and finally, to highly specific assemblies of neurons with complex electrical, coordinated activity in the mature system (Egorov & Draguhn, 2012; Singer, 1995).

Specific to auditory stimulation, adult neuronal oscillations in the delta (~1–4 Hz) and theta (~4–8 Hz) range in primary auditory cortex are phase-locked to the rate and rhythm of auditory stimulus presentation (Gao et al., 2009; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008) and organize spike response to sound input based on the timing of presentation (Canolty et al., 2006; Lakatos et al., 2005). This suggests a role for delta and theta band oscillations in processing and perhaps tracking low-frequency, periodic input. Similarly, delta–theta band oscillations in adult auditory regions have been shown to phase-lock to the temporal dynamics of the speech envelope (Abrams, Nicol, Zecker, & Kraus, 2008; Giraud & Poeppel, 2012; Luo & Poeppel, 2012). This is particularly relevant to the current study because rapid acoustic changes can be reflected in both temporal and spectral envelope shifts. Importantly, measures of speech envelope representation has been shown to be abnormal in school-aged children with language problems (Abrams, Nicol, Zecker, & Kraus, 2009), suggesting a behavioral link. This notion is bolstered by recent data demonstrating that theta, beta and gamma power underlie auditory change detection in sleeping newborns (Isler et al., 2012). Taken together, these data support the idea that oscillatory mechanisms may play a key role in auditory cortical development and information processing, and strongly suggest that oscillatory mechanisms underlie rapid auditory processing development in the first year of life.

Empirical evidence suggests that the timing and strength of synchronized neural activity, such as oscillations, may differ across left and right cortical hemispheres in infants. A developmental time course of hemispheric myelination asymmetry has been observed over the first year of life, beginning at about 3 months-of-age with the left hemisphere having earlier and greater myelination increases than the right in multiple cortices, including auditory regions (Choe et al., 2013; Deoni et al., 2011). The advancement of left-before-right myelination development is consistent with mature microstructure in adult auditory areas, in which left auditory regions show greater white matter volume (Penhune, Zatorre, MacDonald, & Evans, 1996) and greater myelin sheath thickness (Anderson, Southern, & Powers, 1999) as compared to the right. These myelination differences are likely significant for functional auditory processing, particularly for rapid auditory processing, because greater myelination could allow for faster conduction and thereby a greater sensitivity to rapid acoustic change (Zatorre & Belin, 2001). In adults, the left-greater-than-right myelination differences have been hypothesized to be a major factor contributing to functional differences in cross-hemisphere temporal resolution as well as the left lateralization of speech vs. right lateralization of music (Warrier et al., 2009; Zatorre, 2001; Zatorre, Belin, & Penhune, 2002). This hypothesis has been further tested with non-speech stimuli, showing that responses to increased temporal variation are lateralized to the left hemisphere (Jamison, Watkins, Bishop, &

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