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Atypical right hemisphere response to slow temporal modulations in children with developmental dyslexia

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ABSTRACT

Phase entrainment of neuronal oscillations is thought to play a central role in encoding speech. Children with developmental dyslexia show impaired phonological processing of speech, proposed theoretically to be related to atypical phase entrainment to slower temporal modulations in speech (<10 Hz). While studies of children with dyslexia have found atypical phase entrainment in the delta band (~2 Hz), some studies of adults with developmental dyslexia have shown impaired entrainment in the low gamma band (~35–50 Hz). Meanwhile, studies of neurotypical adults suggest asymmetric temporal sensitivity in auditory cortex, with preferential processing of slower modulations by right auditory cortex, and faster modulations processed bilaterally. Here we compared neural entrainment to slow (2 Hz) versus faster (40 Hz) amplitude-modulated noise using fNIRS to study possible hemispheric asymmetry effects in children with developmental dyslexia. We predicted atypical right hemisphere responding to 2 Hz modulations for the children with dyslexia in comparison to control children, but equivalent responding to 40 Hz modulations in both hemispheres. Analyses of HbO concentration revealed a right-lateralised region focused on the supra-marginal gyrus that was more active in children with dyslexia than in control children for 2 Hz stimulation. We discuss possible links to linguistic prosodic processing, and interpret the data with respect to a neural 'temporal sampling' framework for conceptualizing the phonological deficits that characterise children with developmental dyslexia across languages.

Introduction

The speech signal carries information at multiple temporal scales, and the brain processes both slow and faster energy modulations simultaneously as part of speech encoding. Experimental studies with adults reveal that hierarchically-nested cortical oscillations at the rates of delta (~1–3 Hz), theta (~4–8 Hz), beta (~15–30 Hz) and gamma (>30 Hz) track the intensity or amplitude modulations in speech in a remarkably faithful way (e.g., Luo and Poeppel, 2007; Morillon et al., 2012; Luo et al., 2010; see Giraud and Poeppel, 2012, for a recent overview). Neuronal cortical oscillations provide a mechanism for the *multi-time resolution* of the speech signal (Poeppel, 2003). Oscillating brain rhythms reflect excitability cycles, namely the concentration of neuronal electrical discharges to particular phases of a temporal cycle. This enables cell networks to align their high excitability rhythmic phase to modulation peaks in the ongoing signal, a process called phase alignment (neuronal entrainment). Phase entrainment enables the brain to encode the amplitude modulations at different temporal rates in speech *in parallel* (Doelling et al., 2014; Gross et al., 2013; Peelle et al., 2013; Park et al., 2015). Across languages, children with developmental dyslexia show impaired processing of phonology (impairments in processing speech sound structure; see Ziegler and Goswami, 2005). A neural oscillatory framework for understanding this 'phonological deficit' in dyslexia across languages based on atypical neuronal entrainment has been proposed: Temporal Sampling theory (Goswami, 2011).

Temporal sampling theory was motivated by the neural multi-time resolution models of speech processing developed by Poeppel and his colleagues (Poeppel, 2003; Poeppel et al., 2008). Poeppel and others (Doelling et al., 2014; Gross et al., 2013) demonstrated that acoustic events such as amplitude *rise times* (energy increases in the signal, which act as auditory "edges") phase-reset ongoing endogenous oscillatory activity, enabling phase alignment. Children with dyslexia are impaired in rise time discrimination across languages (Goswami, 2015, for a recent summary). Accordingly, temporal sampling theory proposed that atypical neural entrainment to AMs < 10 Hz, present from birth and mediated by impaired sensory discrimination of amplitude rise times, might affect language acquisition and phonological development in dyslexia from infancy onwards. Studies of phonological development show that the emergence of 'phonological awareness' in all children develops in an hierarchical fashion across languages, from larger (e.g., syllables) to smaller (e.g. phonemes) units. Cortical oscillations at different temporal rates yield acoustic information relevant to

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this *phonological structure* of speech, with *delta* band information related to the extraction of syllable stress patterns, *theta* band information related to the extraction of syllabic information, *beta* band information related to onset-rime units (to divide a syllable into the linguistic units of *onset* and *rime*, segment at the vowel, e.g. *s-ing, st-ing, str-ing*), and *low gamma* band information related to phonetic information (see Ghitza and Greenberg, 2009; Ghitza et al., 2012; Poeppel, 2014; Leong and Goswami, 2015). There is also hemispheric specialization, with a right-hemisphere preference for slower temporal modulations (e.g., Boemio et al., 2005). As oscillatory phase entrainment is implicated in both bottom-up processing of low-level acoustic cues in the signal (Howard and Poeppel, 2010; Gross et al., 2013), and in top-down processing of high level cues such as semantic information (Peelle et al., 2013; Gross et al., 2013), children with functionally atypical phase entrainment would process the speech signal in a different way to typically-developing children. This could lead to the phonological system developing differently in children with developmental dyslexia, with lexical phonological representations encoding subtly different acoustic information.

Given that natural child-directed speech (CDS, e.g. nursery rhymes) and infant-directed speech (IDS) are highly rhythmic, accurate phase entrainment to *slower* temporal modulations might be expected to be critical developmentally for setting up the language system (Goswami, 2015). In infancy and early childhood, when semantic and pragmatic knowledge are relatively sparse, bottom-up phase entrainment to prosodic structure might be of primary importance (Kovelman et al., 2012; Goswami and Leong, 2013). The role of phase entrainment in the accuracy of speech processing by infants and children has yet to be studied in any depth. However, recent modelling of the CDS speech signal (English nursery rhymes) has revealed a core role for amplitude modulations (AMs) at the delta rate in the phonological hierarchy. Using an amplitude demodulation approach, Leong and Goswami (2015) characterised the acoustic statistical structure of English nursery rhymes as a Spectral-Amplitude Modulation Phase Hierarchy (S-AMPH) model. Their modelling revealed that the core statistical dependencies in CDS could be described by 3 nested tiers of AM which were found across all spectral bands, at temporal rates of AM centred on ~2 Hz, ~5 Hz and ~20 Hz (these temporal rates would correspond to neuronal oscillations in the delta, theta and beta ranges). The AM tiers were arranged hierarchically in the speech signal, with delta (2 Hz) as the master oscillator. Indeed, analyses of infant-directed speech (IDS) reveal that the greatest energy in the speech signal is in the delta band, suggestive of a core role for slow temporal modulations in initial language learning (Leong et al., 2014). The dominance of energy modulations in the delta band also provides an interesting contrast to adult-directed speech (ADS), in which theta band modulations dominate (~5 Hz). The modulation peak in the theta band in ADS has caused theta to be described as the master oscillator for speech processing by adults (e.g., Ghitza, 2011). Logically, however, as all studies of ADS to date have used highly literate participants, the shift in maximal energy from the delta band (in speech to infants and young children) to the theta band (in speech to adults) could reflect changes in neural speech processing that are a product of learning to read.

Available studies of oscillatory entrainment in infants and children have so far focused on non-speech stimuli, and have usually compared entrainment to amplitude-modulated noise at the two temporal rates for linguistic processing originally identified by multi-time resolution models, theta (putative syllable rate) and gamma (putative phonetic rate, see Poeppel, 2003; Poeppel et al., 2008). These non-speech stimuli typically measure neural entrainment by recording the *amplitude following response* of the brain oscillations (auditory steady state response, ASSR). Studies using electroencephalography (EEG) and functional near infrared spectroscopy (fNIRS) have revealed that even newborn (German) infants show an ASSR to amplitude-modulated noise at the contrasting rates of 3 Hz (~ delta/theta band) and 40 Hz (gamma band, Telkemeyer et al., 2009, 2011). Furthermore, the ASSR is right-lateralised for the slower rate in both newborn and older infants, whereas for the faster (gamma) rate the ASSR is bilateral. This suggests that asymmetric processing of auditory temporal input is a core feature of human speech processing, with preferential right-lateralized processing of slower temporal modulations present from (or before) birth. Meanwhile, a recent EEG study of Dutch-speaking 5-year-old children recorded the ASSR to speech-weighted noise stimuli amplitude-modulated at 4 Hz or 20 Hz, designated the 'syllable' and 'phoneme' rates by the authors (Vanvooren et al., 2014). Vanvooren and colleagues reported a right hemisphere preference for processing the syllable-rate modulations in these pre-reading children, and a symmetric pattern for phoneme-rate modulations.

We are only aware of one published study of phase entrainment to *speech stimuli* by children without learning difficulties. Power and colleagues designed an EEG speech paradigm based on rhythmic repetition of the syllable "ba" at a 2 Hz rate. English-speaking children either saw a 'talking head' repeating "ba", so that both visual and auditory information was present (audio-visual or AV condition), saw the talking head without sound, so that only visual information was present (V), or heard the auditory stimulus stream in the absence of visual stimulation (A). The children were asked to detect occasional rhythmic violations in each condition (A, V, AV). Power et al. (2012) found significant oscillatory entrainment at the stimulation rate (delta, 2 Hz) in all three conditions, and also significant entrainment at the theta rate in the auditory and AV conditions, consistent with the predictions of multi-time resolution models of speech processing (i.e., theta entrainment was important in processing this syllabic input). Furthermore, Power et al. reported that individual differences in the strength of *theta* entrainment (measured by inter-trial coherence or phase consistency) was related to the development of reading in their typically-developing sample. Higher theta phase consistency was associated with better reading. Hemispheric differences were not measured.

Studies of oscillatory phase entrainment are more frequent in the developmental dyslexia literature, although most studies to date have utilised adult participants and have focused on the fast gamma oscillations thought to support phonetic analysis. For example, Lehongre and colleagues used amplitude-modulated white noise at rates that increased incrementally from 10 to 80 Hz and the ASSR to study neural entrainment in French-speaking adults with and without dyslexia. Of particular theoretical interest were oscillations in the low gamma band (25–35 Hz), thought to reflect optimal phonemic encoding. Both dyslexic and control participants showed significant phase entrainment, but the typical adult pattern of left-dominant gamma entrainment was shown by the control participants only. Lehongre et al. (2011) argued that their data suggested a focal (left-lateralised) impairment in the selective extraction and encoding of phonemic information in developmental dyslexia. However, it is impossible to know whether this selective impairment was present earlier in childhood, or whether it arose because of the severely reduced reading experience (and associated reduced grapheme-phoneme recoding experience) that accompanies being dyslexic (see Goswami, 2015). In a second study with French-speaking adult dyslexics using conversational speech (viewing a movie), Lehongre et al. (2013) replicated the finding of atypical left hemisphere responding to gamma band information, but did not find group differences in the neural response to theta- or delta-band information in pre-determined regions of interest (Heschl's gyrus and planum temporale). However, it is logically possible that atypical responding to slower modulations in speech may have been present earlier in development and/or in other brain regions. Meanwhile, Poelmans et al. (2012) used the same nonspeech stimuli as Vanvooren et al. (2014) to study the ASSR to 4 Hz and 20 Hz stimulation in Dutch-speaking adults with and without dyslexia. They reported a significant group x laterality effect for the 20 Hz stimulus only, also concluding that cortical processing of phoneme-rate modulations rather than syllable-rate modulations was impaired in developmental