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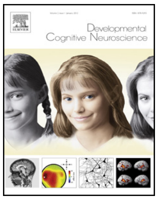

What changes in neural oscillations can reveal about developmental cognitive neuroscience: Language development as a case in point

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ABSTRACT

EEG is a primary method for studying temporally precise neuronal processes across the lifespan. Most of this work focuses on event related potentials (ERPs); however, using time-locked time frequency analysis to decompose the EEG signal can identify and distinguish multiple changes in brain oscillations underlying cognition (Bastiaansen et al., 2010). Further this measure is thought to reflect changes in inter-neuronal communication more directly than ERPs (Nunez and Srinivasan, 2006). Although time frequency has elucidated cognitive processes in adults, applying it to cognitive development is still rare. Here, we review the basics of neuronal oscillations, some of what they reveal about adult cognitive function, and what little is known relating to children. We focus on language because it develops early and engages complex cortical networks. Additionally, because time frequency analysis of the EEG related to adult language comprehension has been incredibly informative, using similar methods with children will shed new light on current theories of language development and increase our understanding of how neural processes change over the lifespan. Our goal is to emphasize the power of this methodology and encourage its use throughout developmental cognitive neuroscience.

In the current understanding of cognitive neuroscience, it is widely accepted that human behavior and cognition arise through communications between and within complex neuronal networks (Fuster, 1997; Sauseng and Klimesch, 2008; Varela et al., 2001). Very little is known about how these communications develop over the lifetime for even simple cognitive tasks. The rapid dynamic nature of these processes cannot be captured by slow moving changes in the BOLD signal with fMRI. Human scalp EEG, however, can record activity related to a large number of highly synchronized neurons in the cortex from the scalp. From these data, we can make inferences about how and when large-scale networks are engaged during task performance. Current advances in data analysis tools, processing capabilities and our understanding of systems neuroscience has led to an increased interest in the synchronization and desynchronization of neuronal oscillations underlying the EEG and what they can reveal about human cognition. To date, the bulk of the work on this topic focuses on adult cognition, despite the incredible potential that this method holds for developmental cognitive neuroscience. Expanding this work to children can greatly advance our understanding of how neuronal communication changes with development.

1. Event related potentials (ERPs) compared to neuronal oscillations

The most common use of EEG to study cognitive functions is through ERPs. ERPs are derived by epoching the

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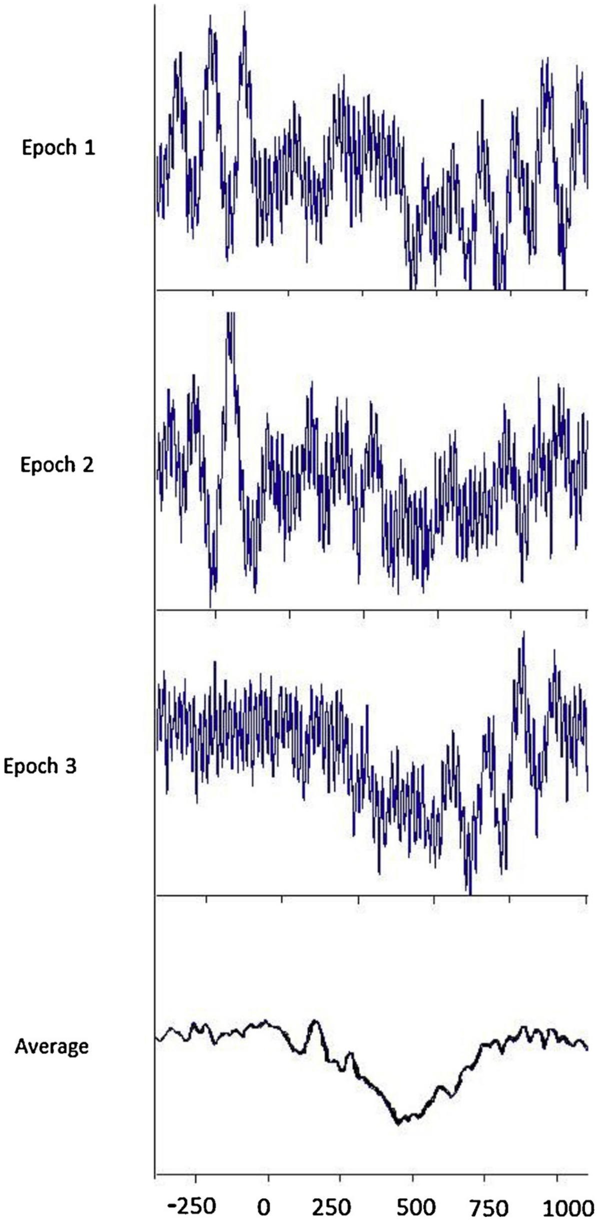

Fig. 1. Three epochs from an ongoing EEG and their average.

ongoing EEG at the point of stimulus presentation then averaging these epochs together to form a stable waveform (see Fig. 1). These waveforms contain predictable peaks related to various cognitive functions (e.g., P300, N400). Comparisons of the amplitude, topography and timing of these peaks across conditions result in inferences about underlying differences in neuronal engagement.

For decades, ERPs have provided a wealth of information about developmental changes in the neuronal underpinnings of cognitive functions. For instance, ERPs have informed our understanding of how infants differentiate phonemes (e.g., Conboy et al., 2008; Rivera-Gaxiola et al., 2012), toddlers learn words (e.g., Torkildsen et al., 2009; Torkildsen, 2006, 2008) and toddlers and young children process syntax (e.g., Oberecker and Friederici, 2006; Oberecker et al., 2005). However, these findings only tell one part of the story because, while the averaging method used to calculate the ERP increases the signal-to-noise ratio in the EEG, it also has significant limitations. First, averaging the EEG attenuates or removes important non-stimulus locked changes in oscillatory activity thought to underlie interneuronal communication (Nunez and Srinivasan, 2006). As a result, ERPs only reveal a portion of the changes in the EEG related to stimulus presentation. Second, differences in ERP components can be the result of many factors that are difficult to tease apart. For example, the N400 amplitude is influenced by a word's concreteness, age of acquisition, and frequency, as well as test language and task differences (i.e., the number of repetitions of a word; Vigliocco et al., 2011). Decomposing the oscillations comprising the ERP and analyzing their underlying frequencies retains time resolution near that of the ERP yet can often better differentiate simultaneous processes that may originate in similar cortical areas to identify these influences (Bastiaansen and Hagoort, 2006; Maguire et al., 2010). As a result, time frequency analysis can compliment and expand upon ERP findings.

2. How to measure changes in neuronal oscillations

The EEG is generally modeled as overlapping sine waves of different frequencies which can be decomposed into its underlying signals (see Fig. 2). Using a time frequency analysis to perform this decomposition, one can derive three important changes in the EEG: (1) magnitude, or amplitude, of the response, (2) frequency, or rate, of the response and (3) phase angle with respect to stimulus onset. Changes in one or more of these EEG characteristics in relation to a stimulus provide information about the underlying neuronal networks. Different time frequency measurements address these potential changes.

Two common measurements include phase resetting changes (sometimes called 'evoked' changes) and magnitude changes (sometimes called 'invoked' changes). *Phase resetting* occurs when the onset of a stimulus results in the ongoing oscillations resetting so they all occur at the same angle (see Fig. 3a). Because these oscillations are at the same angle they do not average out in the traditional ERP analysis; instead they remain robust during the averaging process and are the primary source of prominent ERP peaks. *Magnitude changes* occur when a particular frequency's amplitude increases in response to a stimulus without corresponding changes in the phase angle. This type of change is thought to relate to the activation of additional neural assemblies firing at the same frequency, or neuronal synchrony, resulting in an increase in the amplitude of the EEG oscillations at that frequency. These changes can be studied at the trial, study, or group level. Regardless of the size of the magnitude increase, because these responses are not phase-locked they may average out or attenuate in the ERP (see Fig. 3b). Magnitude changes are often discussed in terms of changes in *power*. For example, an "increase in theta power" means the magnitude of the theta frequency increased without phase locking. Additional measures of power are coherence within and between frequencies