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Delta, theta, beta, and gamma brain oscillations index levels of auditory sentence processing

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ABSTRACT

A growing number of studies indicate that multiple ranges of brain oscillations, especially the delta (δ, <4 Hz), theta (θ, 4–8 Hz), beta (β, 13–30 Hz), and gamma (γ, 30–50 Hz) bands, are engaged in speech and language processing. It is not clear, however, how these oscillations relate to functional processing at different linguistic hierarchical levels. Using scalp electroencephalography (EEG), the current study tested the hypothesis that phonological and the higher-level linguistic (semantic/syntactic) organizations during auditory sentence processing are indexed by distinct EEG signatures derived from the δ, θ, β, and γ oscillations. We analyzed specific EEG signatures while subjects listened to Mandarin speech stimuli in three different conditions in order to dissociate phonological and semantic/syntactic processing: (1) sentences comprising valid disyllabic words assembled in a valid syntactic structure (real-word condition); (2) utterances with morphologically valid syllables, but not constituting valid disyllabic words (pseudo-word condition); and (3) backward versions of the real-word and pseudo-word conditions. We tested four signatures: band power, EEG–acoustic entrainment (EAE), cross-frequency coupling (CFC), and inter-electrode renormalized partial directed coherence (rPDC). The results show significant effects of band power and EAE of δ and θ oscillations for phonological, rather than semantic/syntactic processing, indicating the importance of tracking δ- and θ-rate phonetic patterns during phonological analysis. We also found significant β-related effects, suggesting tracking of EEG to the acoustic stimulus (high-β EAE), memory processing (θ–low-β CFC), and auditory-motor interactions (20-Hz rPDC) during phonological analysis. For semantic/syntactic processing, we obtained a significant effect of γ power, suggesting lexical memory retrieval or processing grammatical word categories. Based on these findings, we confirm that scalp EEG signatures relevant to δ, θ, β, and γ oscillations can index phonological and semantic/syntactic organizations separately in auditory sentence processing, compatible with the view that phonological and higher-level linguistic processing engage distinct neural networks.

Introduction

Cortical oscillatory activity plays a key role in conveying and controlling neural information across the brain, whereby various fundamental cognitive functions, such as attention, learning, memory, and decision-making, are realized (Ward, 2003; Siegel et al., 2012). Brain oscillations are conventionally divided into several frequency ranges: delta (δ, <4 Hz), theta (θ, 4–8 Hz), alpha (α, 8–13 Hz), beta (β, 13–30 Hz), and gamma (γ, >30 Hz) (Ward, 2003). Numerous studies have shown that certain cognitive functions are related to oscillations in multiple frequency ranges. For example, attention is related to changes in α and γ activities (Klimesch, 2012; Jensen et al., 2007), whereas working memory and long-term memory processes involve θ, β, and γ activities (Ward, 2003; Jensen et al., 2007; Fell and Axmacher, 2011). An important topic of human cognitive neuroscience in recent years considers how language is processed via coordination of brain oscillations. The current paper focuses on the auditory modality, and deals with how brain oscillations underpin auditory sentence processing. Previous studies have accumulated evidence that speech and auditory sentence processing are associated with multiple ranges of brain oscillations, including both low-frequency components, such as δ and θ oscillations, and high-frequency components, such as β and γ oscillations (see reviews: Giraud and Poeppel, 2012; Lewis et al., 2015).

Abbreviations: EEG, Electroencephalography; MEG, Magnetoencephalography; EAE, EEG–acoustic entrainment; CFC, Cross-frequency coupling; rPDC, Renormalized partial directed coherence; MI, Modulation index; SUS, Semantically unpredictable sentence; WM, Working memory.

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For low-frequency components (i.e., δ and θ), recent findings showed that the phase information of the δ and θ oscillations are involved in speech perception. The δ and θ (i.e., 1–8 Hz) phase measured by magnetoencephalography (MEG) can be used to successfully classify different auditory sentences attended to by subjects (θ phase in Luo and Poeppel, 2007; δ and θ phase in Cogan and Poeppel, 2011). In an electroencephalography (EEG) study, the phase restricted to 2–9 Hz (which overlaps the δ and θ bands) can successfully classify different American English consonants (Wang et al., 2012). In connection with such findings on the importance of δ/θ phase, two other recent neurophysiological studies have found that entrainment (i.e., phase-locking) of δ and θ brain oscillations to the speech envelope at the corresponding δ and θ amplitude-modulation rates may underpin speech intelligibility and serve as one of the neural mechanisms of speech processing (Peelle et al., 2013; Doelling et al., 2014). Peelle et al. (2013) found that the degree of θ (4–7 Hz) MEG-envelope entrainment was related to sentence intelligibility observed in the left auditory cortex and middle temporal gyrus. Doelling et al. (2014) artificially removed the δ- and θ-rate (2–9 Hz) envelopes of sentences in various acoustic spectral bands and consequently found that the δ–θ MEG-envelope entrainment was suppressed, accompanied by a reduction in sentence intelligibility. The correlation between brain–acoustic entrainment in the δ–θ range and speech intelligibility thus emphasizes the importance of δ and θ brain oscillations in auditory sentence processing (see review by Ding and Simon, 2014).

Besides involvement in brain–acoustic entrainment, the power of low-frequency components was also found to be important for speech processing. For instance, Peña and Melloni (2012) used a cross-linguistic design to compare the EEG oscillations elicited from Italian and Spanish speakers while listening attentively to Italian, Spanish, and Japanese utterances played both forward and backward. This study found that, in both Italian and Spanish subjects, θ power was significantly higher when listening to forward than to backward utterances, regardless whether or not the language was native. The finding that forward utterances elicit higher θ power than backward utterances, even for a non-native language, thus indicates that θ power may be involved in tracking syllable patterns (Peña and Melloni, 2012). In a more recent MEG study (Ding et al., 2015), similar results were found which showed that, when listening to Chinese sentences with syllable rate of around 4 Hz, both native Chinese or English listeners showed significantly higher 4-Hz MEG power for forward sentences than for the backward versions. Considering that backward utterances preserve properties that are closely matched to the acoustic complexity of speech utterances but cause serious phonological distortions (Binder et al., 2000; Saur et al., 2010; Gross et al., 2013), syllabic tracking in speech utterances may involve a higher degree of phonological analysis compared to backward utterances, even in a non-native language. Studies have found that θ oscillations are also involved in lexical–semantic retrieval (Bastiaansen et al., 2008) and in syntactic processing during sentence perception (Bastiaansen et al., 2002), the former involving retrieval of long-term semantic knowledge and the latter involving working memory processing.

For high-frequency components, such as β and γ oscillations, there is evidence that brain oscillations in this range are involved in different linguistic processes. A recent MEG study (Alho et al., 2014) investigated the inter-areal phase synchronies of high-β (β2, 20–30 Hz) and γ oscillations between the auditory and motor cortices during active and passive listening to phonologically valid but meaningless mono-syllables in both clean and noisy environments. It showed that the left-hemispheric inter-areal β2 synchronies were significantly greater during syllable listening in noisy than in clean environments and that such synchronies were positively correlated with syllable identification accuracy. Furthermore, inter-areal γ synchronies were found to be greater during active than passive listening. This indicates the mediation of phonological categories in speech by inter-areal connectivity between auditory–sensory and motor regions via β2 and γ oscillations. For higher linguistic-level processing, β oscillations were reported to be involved in syntactic processing, showing higher EEG β power for syntactically correct than syntactically unstructured and word category violated sentences (Bastiaansen et al., 2010; also reviews by Lewis and Bastiaansen, 2015; Lewis et al., 2015). In addition, γ oscillations were reported to be involved in lexico-semantic retrieval (Lutzenberger et al., 1994; Pulvermüller et al., 1996). These studies found significant increases in γ oscillations when subjects actively perceived real-word compared to pseudo-word stimuli in both visual (Lutzenberger et al., 1994) and auditory (Pulvermüller et al., 1996) modalities, which is consistent with the critical role of γ activity in long-term memory processing (Ward, 2003).

In addition to the respective roles of δ, θ, β, and γ oscillations, the hierarchical organization between the low-frequency and high-frequency oscillations, termed cross-frequency coupling (CFC), serves as another important parameter for speech processing (Fell and Axmacher, 2011; Lisman and Jensen, 2013). Here, we focus on phase-power CFC, in which the power of high-frequency oscillations is controlled by the phase patterns of low-frequency oscillations (Tort et al., 2008). It has been found that θ–β/γ CFC increased significantly across a range of human cortical regions during various cognitive tasks, including language-related tasks, such as active/passive listening to phonemes and words, word production, visual reading, and so on (Canolty et al., 2006). The phenomenon of θ–β/γ CFC increase has been interpreted in other studies as the neural mechanism for memory processing, including encoding and retrieval of long-term memory and working memory maintenance in both non-human mammals (Tort et al., 2008, 2009; Shirvalkar et al., 2010) and human beings (Mormann et al., 2005; Sauseng et al., 2009; Axmacher et al., 2010; Friese et al., 2013; Köster et al., 2014; Kaplan et al., 2014). It is likely, therefore, that θ–β/γ CFC is related to high-level linguistic processes like phonological working memory maintenance and retrieval of lexical–semantic information, or even sentence-level processes related to memory retrieval or encoding (e.g., contextual semantic integration and syntactic processing). Furthermore, it has recently been suggested that θ–β/γ CFC supports the hierarchical binding of both long-duration (such as syllables and long phonemes, e.g., long-vowels, at θ-scale) and short-duration (such as short phonemes, e.g., consonants and short-vowels, at β/γ-scale) phonological information during speech analysis (Giraud and Poeppel, 2012; Gross et al., 2013). Besides θ–β/γ CFC, the coupling between δ and θ oscillations (δ–θ CFC) may also be important. δ–θ CFC was found to be higher when listening to forward than to backward utterances, indicating a possible role of hierarchical binding between even longer-duration information of prosody or phrases/words (at δ-scale) and the θ-scale information in speech perception (Gross et al., 2013), although one should be cautious when interpreting the δ–θ CFC effects due to the close frequency ranges between δ and θ oscillations that could cause intrinsic coupling effects mathematically.

In spite of the abundant findings on brain oscillations to describe language processing as reviewed above, few studies have examined these oscillatory indices for different linguistic hierarchical levels simultaneously. How brain oscillations index and separate processes at these levels therefore remains obscure. The current study aims at revealing oscillatory EEG indices for phonological and higher-level linguistic (semantic/syntactic) processing during listening to auditory sentences in Mandarin. We used three types of continuous utterance stimuli in Mandarin in order to dissociate the effects caused by acoustics, phonology, and the higher linguistic levels: (1) sentences consisting of meaningful disyllabic words assembled with a valid syntactic structure (real-word condition); (2) utterances with morphologically valid syllables, but no valid disyllabic words (pseudo-word condition); and (3) backward versions of both the real-word and pseudo-word utterances ('non-speech' condition). In this design, real-word and pseudo-word utterances can be distinguished by their differences in semantic content. For example, in the real-word condition, the syllable pair, '喜' and '欢', constitutes a disyllabic word, '喜欢' ('enjoy'), while in the pseudo-word condition, the two successive syllables, '书' and '实', do

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