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Identifying the relationship between oscillatory dynamics and event-related responses

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ABSTRACT

Event related potentials (ERPs) and time frequency analysis of the EEG can identify the temporally distinct coordination of groups of neurons across brain regions during sentence processing. Although there are strong arguments that ERP components and neural oscillations are driven by the same changes in the neural signal, others argue that the lack of clear associations between the two suggests oscillatory dynamics are more than just time frequency representations of ERP components, making it unclear how the two are related. The current study seeks to examine the neural activity underlying auditory sentence processing of both semantic and syntactic errors to clarify if ERP and time frequency analyses identify the same or unique neural responses. Thirty-nine adults completed an auditory semantic judgment task and a grammaticality judgment task. As expected, the semantic judgment task elicited a larger N400 and greater increase in theta power for semantic errors compared to correct sentences and the syntactic judgment task elicited a greater P600 and beta power decrease for both grammatical error types compared to syntactically correct sentences. Importantly, we identified a significant relationship between the N400 and P600 ERPs and theta and beta oscillatory dynamics during semantic and syntactic processing. These findings suggest that ERPs and neural oscillations measure similar neural processes; however, unaccounted for variance may indicate that neural oscillations provide additional information regarding fluctuations in power within a given frequency band. Future studies that vary semantic and syntactic complexity are necessary to understand the cognitive processes that are indexed by these oscillations.

1. Introduction

Natural language comprehension is a fast-paced process that requires rapid integration and unification of lexical items to create a cohesive understanding of what is being communicated (Lam et al., 2016; Montgomery et al., 2015; Marslen-Wilson and Tyler, 1980; Borovsky et al., 2012). During comprehension, listeners must integrate information pertaining to the prosody, meaning, structure, and pragmatics of the incoming message with millisecond precision.

Event related potentials (ERPs) and oscillatory dynamics are two measures implemented to identify the temporally distinct coordination of groups of neurons across brain regions required for sentence processing (Lam et al., 2016). How these two measures of the neural correlates underlying cognitive processes relate to one another remains unclear. The current study seeks to not only examine the neural activity underlying auditory sentence processing of both semantic and syntactic errors, but to clarify the relationship between event-related and time frequency responses. These findings will clarify if power changes in oscillatory dynamics explain the generation of the N400 and P600 ERPs, or if oscillatory activity and ERPs reflect different neural processes.

There have been strong arguments that ERP components measure the same changes in the neural signal as neural oscillations, but in somewhat different ways (Hagoort et al., 2004; Roehm et al., 2007; Schneider et al., 2016; Davidson and Indefrey, 2007; Bastiaansen et al., 2002). However, others have found that the lack of clear associations between the two suggests oscillatory dynamics are more than just time frequency representations of ERP components (Bastiaansen et al., 2008; Wang et al., 2012; Bastiaansen and Hagoort, 2015), making it unclear how the two are related. Recent research in the field of psycholinguistics has shown a growing interest in time frequency responses as a means of clarifying the neural mechanisms underlying language comprehension (for review, see Hauk et al., 2017). ERPs, while informative, are phase-locked neural responses that are created by averaging across multiple trials within the same condition. An ERP may therefore be the result of an evoked response by an additive

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mechanism, phase-reset of ongoing oscillatory activities, or asymmetric oscillatory activities (Bastiaansen et al., 2012; Mazaheri and Jensen, 2008; van Dijk et al., 2010; Cohen, 2014). On the other hand, oscillatory dynamics, characterized by using event-related synchronization, temporal spectral evolution, or time-frequency representations of power, allows the EEG signal to be decomposed into different frequencies. This decomposition with time frequency analysis can identify induced, non-phase-locked neural responses across multiple frequencies by revealing changes in the amplitude of oscillations induced by stimuli (Bastiaansen et al., 2012; Kielar et al., 2014; Pfurtscheller and Da Silva, 1999).

Related to language, there is a general consensus in the literature that increases in both the N400 and theta frequency occur in response to increased semantic processing demands. The N400 is an ERP component with a negative amplitude over widespread electrodes between approximately 300 to 500 milliseconds (msecs) and occurs in response to semantic errors (Kutas and Federmeier, 2011; Neville et al., 1992; King and Kutas, 1995). The more difficult the semantic information is to integrate into the proceeding text or to retrieve a semantic representation, the greater the N400 response will be (Kutas and Hillyard, 1980; Van Berkum, 2009; Kutas and Federmeier, 2011). Similarly, increases in theta power (4–8 Hz) index semantic aspects of language processing including integration of semantic information (Bastiaansen et al., 2010; Bastiaansen et al., 2002; Davidson and Indefrey, 2007; Hagoort et al., 2004; Hald et al., 2006; Maguire et al., 2010; Wang et al., 2012). Theta has been shown to increase with each incoming word during sentence reading; yet, in the presence of a semantically incongruent word in the sentence, theta power is greater than when the words are semantically congruent (Bastiaansen et al., 2010). Although many studies implementing the same task have highlighted the similarity between the N400 and theta response, conclusions regarding the relationship between the two are mixed. Some studies have concluded that theta power changes might be attributed to the same underlying processing characteristics as the N400 response, while others suggest theta power changes are identifying neural processes beyond those represented by the N400 (Table 1). Davidson and Indefrey (2007) was one of the few to directly compare event-related and time frequency responses, concluding that based on the directionality of response types, an inverse relationship between the N400 and theta existed. However, significant variability remains across studies and therefore a direct comparison of increases in both the N400 and theta is necessary to delineate the relationship between event- related and time frequency responses during semantic processing.

Fewer studies have investigated the relationship between the P600 and beta band (13–30 Hz). The P600, an ERP component that displays a posterior distribution and is typically observed as a positive peak around 500 to 800 msec, is found in response to subject-verb agreement violations, verb or case inflections, and phrase structure violations (for review, see Kutas and Federmeier, 2007). Importantly, the P600 is greater in response to grammatical violations, regardless of their position within a sentence, and grammatical processing more broadly (Davidson and Indefrey, 2007; Hagoort et al., 1993; Osterhout and Holcomb, 1992; Osterhout, 1997). Using time frequency analysis, beta power has been identified as increasing with each word in a visually-presented grammatically correct sentence, but decreases at the point of a syntactic error in a sentence when syntactic unification fails (Bastiaansen et al., 2010; Davidson and Indefrey, 2007). Based on the fact that increases in the P600 have been interpreted as an index of syntactic processing ability and decreases in beta power are argued to reflect syntactic processing difficulty, both the P600 and beta are commonly investigated together (Bastiaansen et al., 2010; Bastiaansen and Hagoort, 2015; Lam et al., 2016). Studies directly comparing changes in the P600 and beta frequency agree that the P600 amplitude is larger in response to errors, while the beta frequency amplitude decreases at an error; however, the relationship between these changes is still widely debated (Table 2). Schneider et al. (2016) reported a

Table 1
Comprehensive review of studies examining changes in both the N400 and Theta band in response to the same study. Although the N400 effect and theta power both increase in response to an error, the arrows here signify that the N400 becomes more negative, while theta power becomes more positive.

Publication	N400	Theta	Paradigm	Conclusion
Davidson and Indefrey (2007)	↓	↑ 3–7 Hz	Participants read sentences that were either correct, contained a subject-verb number agreement error, phrase structure error, or semantic error.	Inverse relationship between event-related and time frequency responses; reflect different aspects of lexical-semantic memory retrieval.
Hagoort et al. (2004)	↓	↑ 4–7 Hz	Participants read sentences that were either correct, contained a world knowledge violation, or semantic violation.	Both are sensitive to semantic integration processes around 400 msec.
Roehm et al. (2007)	↓	↑ 3–5 Hz	Participants judged antonym relations within a sentence context or performed a lexical decision task.	Even superficially distinct ERP effects might be attributed to the same underlying processing characteristics.
Schneider et al. (2016)	↓	↑ 4–8 Hz	Participants listened to sentences that were either correct or contained a syntactic error of either omission or intrusion.	In children, a theta increase and N400 were both present between 350 and 450 msec, related to semantic integration; however, no correlation was present.
Bastiaansen et al. (2008)	↓	↑ 4–7 Hz	Participants completed a lexical decision task with single word auditory or visual stimuli.	The lack of clear associations between the theta and N400 findings suggests that oscillatory responses are more than just time frequency representations of the ERP.
Bastiaansen et al. (2002)	↓	↑ IAF 4–6 Hz	Participants read sentences containing either a syntactic violation, semantic violation, complex pronomial reference, or were correct.	Latencies of changes in theta fall roughly in the same time window of the N400, therefore, power increases are related to some aspect of word processing.
Wang et al. (2012)	↓	↑ 2–5 Hz	Participants read low constraining, high constraining, and semantically incongruent sentences.	Theta differences are only partly produced by changes in the ERP. Theta may not be related to error detection (like the N400), but rather may be related to other aspects of language comprehension.
Bastiaansen and Hagoort (2015)	↓	↑	Participants read Dutch sentences that were either correct, contained a semantic error, syntactic error, were randomized to remove syntactic structure, or syntactically correct, but semantically uninterpretable.	Scalp topography differences suggest that theta power differences are a truly non-phase-locked, oscillatory phenomenon; however, both are still related to retrieval of lexical semantic information.