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Independent contributions of theta and delta time-frequency activity to the visual oddball P3b☆,☆☆

Matthew D. Bachman[a,*], Edward M. Bernat[b,*]

[a] Center for Cognitive Neuroscience, Duke University, USA
[b] Department of Psychology, University of Maryland, College Park, USA

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ABSTRACT

A growing body of work suggests that the P300 (P3) event-related potential (ERP) component is better understood as a mixture of task-relevant processes (Polich, 2007). This converges with earlier time-frequency work suggesting that the P3b is primarily composed of centroparietal delta (0.5–3 Hz) and frontocentral theta (3–7 Hz) activity. Within this study (N = 229), we hope to re-affirm these prior ideas and expand upon them in several crucial ways, reassessing how delta and theta contribute to the visual oddball P3b through the lens of several recent decades of additional P3b research. We provide a comprehensive assessment of how theta and delta time-frequency activity contribute to several common variants of the time-domain P3b, specifically measuring the target and non-target P3b, as well as differences between targets and non-targets, target-to-target interval (TTI), and target habituation. Results replicate and extend earlier work indicating that delta and theta account for a majority of variance in both the target and non-target P3b as well as their respective amplitude differences. They also newly indicate that theta and delta activity can have unique contributions to TTI differences and target habituation effects. Results in target habituation particularly demonstrate how time-frequency analyses can disentangle nuanced changes in P3b activity, shedding new light on these complicated phenomena. Findings suggest that delta and theta measures index separable processes occurring during the P3b, and provide additional support for the idea that they index theoretical frontocentral and centroparietal P3 subcomponents.

1. Introduction

A substantial body of early work investigated delta and theta activity underlying the target P3b component, advancing the idea that event-related potentials (ERPs) can be understood as a superposition of multiple subcomponents, separable by frequency (Başar, 1980; Başar-Eroglu et al., 1992; Karakaş et al., 2000a; Demiralp et al., 2001b; Güntekin and Başar, 2016). This work undoubtedly contributed towards modern interpretations of the P300 (Polich, 2007). However, since then there has been substantial refinement of theoretical and empirical considerations of the P3, as well as advances in time-frequency approaches. The goal of the present study is to provide a more comprehensive examination of how delta and theta activity contribute to the visual oddball P3b, testing several core ideas regarding their relationship and using the same time-frequency measurement approach across all comparisons. To address this, we first replicate and extend widely studied manipulations (targets, non-targets, and non-target comparisons), and then apply this framework to target-to-target intervals and P3b habituation. The findings provide an updated assessment, and additional evidence, supporting the hypothesis that theta and delta activity can usefully index core frontocentral and centroparietal subcomponents widely understood to underlie the P3b.

1.1. An overview of P300

The P300 (P3) event-related potential (ERP) has evaded a comprehensive explanation despite its lengthy study. It's prevalence among cognitive tasks, sensitivity to multiple experimental conditions (Kok, 2001), and variable time course (Verleger, 1997), has spurred substantial research into its neural and conceptual origins (Donchin, 1981; Kok, 2001; Verleger et al., 2005; Polich, 2007). However, fundamental questions remain about the nature of the processes underlying its generation, undermining a satisfactory understanding of both its relationship to cognitive processes and clinical applications. Over the years, a number of models have been developed attempting to reconcile these difficulties. One influential theory frames it as a resulting process

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* Corresponding authors.
E-mail addresses: matthew.bachman@duke.edu (M.D. Bachman), ebernat@umd.edu (E.M. Bernat).

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while updating contextual memory relevant to the task, with higher amplitudes resulting when stimuli differ from previous trials (Donchin, 1981). Other theories have named the P3 as a link between perceptual analysis and response initiation (Verleger et al., 2005), or a measure of event categorization (Kok, 2001). The variation in both number and content of these theories highlights the difficulty in developing a singular definition of P3 function, but there is a growing body of work suggesting that the presumption that the P3 is a unitary process may be overlooking critical and complex aspects of its generation and function.

1.2. P300 subcomponents

Work across multiple areas suggests that P3 can be better understood as a mixture of processes rather than a singular event. One important distinction separates the P3 into two subtypes: an earlier P3a component typically elicited by novel and nogo-like stimuli, and the more classic P3b component, which is elicited by targeted stimuli with a later time-range (Polich, 2007). Although they are typically categorized by different stimuli and time ranges, they additionally contrast in other crucial manners. The P3b has a centroparietal topographic distribution and has been linked to stimulus evaluation, while the P3a has a more frontocentral topographic distribution and has been linked to attentional or orienting responses (He et al., 2001; Spencer et al., 2001; Gaeta et al., 2003; Yago et al., 2003). While early work noted the differences between these components, it was initially unclear whether they were being accurately classified as subtypes of a similar ERP, or were functionally dissimilar components with a broadly similar time-course. Several studies in pursuit of this answer point to both components sharing the same underlying mechanisms. Spatiotemporal principal component analysis has been used to demonstrate that conventional time domain P3a and P3b measures each contain both a frontocentral and centroparietal component, which are weighted differentially in the conventional measures (Spencer et al., 1999, 2001). Work based on independent component analysis has similarly found that the P3a and P3b are each composed of two subcomponents that differ spatially and are weighted differentially (Debener et al., 2005). Collectively these findings suggest that the same two components are active in processing both novel and target stimuli, but that the greater relative activation of one versus the other based on context is responsible for the observed P3a and P3b differences. This work has been more empirical than theoretical, but has created the opportunity to reframe our understanding of the P3 through these unique neurocognitive processes. However, this work has made clear that work with either P3 component must fundamentally address these subcomponents or risk overlooking these underlying mechanisms.

1.3. Time-frequency methodology and the P300

Most research on P3 components has been done with time-domain methodology, where components are defined by the amplitude occurring within specific temporal start and end points. However, this approach has drawbacks in disassociating between temporally overlapping activity in ERPs. This is particularly relevant when studying the P3, as these measures may contain energy from preceding ERPs such as the N2 or FN that may continue during the time of the P3. However, time-frequency (TF) approaches can characterize activity simultaneously in time and frequency, providing measures that are separated in frequency, but which overlap in time. A number of efforts have now demonstrated that energy in centroparietal delta (< 3 Hz) and frontocentral theta (3–7 Hz) frequencies can explain the majority of variance in P3 from oddball tasks (Kolev et al., 1997; Başar et al., 1999; Spencer and Polich, 1999; Karakaş et al., 2000a, 2000b; Yordanova et al., 2000; Başar-Eroglu and Demiralp, 2001; Başar et al., 2001; Demiralp et al., 2001a, 2001b). Separable contributions from theta and delta activity also account for the majority of variance in several other ERP components, such as the error-related negativity (Yordanova et al., 2004), feedback-related negativity (Gehring and Willoughby, 2004), and nogo N2 (Kirmizi-Alsan et al., 2006; Barry, 2009).

A majority of work employing time-frequency analysis has utilized wavelet time-frequency transforms, which smear activity in time at low frequencies and in frequency at high frequencies (Bernat et al., 2005). In recent work from our group, we have employed the reduced interference distribution (RID) from Cohen's class of time-frequency transforms which do not smear activity in this way, providing instead a uniform time-frequency resolution at both low and high frequencies (Bernat et al., 2005). Using this approach, we have characterized separable theta and delta activity underlying ERP components from several common tasks, including go/no-go N2 and P3 (Harper et al., 2014, 2016), gambling feedback FN and P3 (Bernat et al., 2011, 2015; Foti et al., 2015), and error-related negativity (Bernat et al., 2005; Hall et al., 2007). This approach has provided improved time and frequency support, allowing a closer investigation of unfolding theta and delta activity in the first 500 ms of the ERP, and how they relate to conventional P2, N2, and P3 ERP components. This work has supported inferences that earlier frontocentral theta relates more to narrow salience processing, and delta to more sustained and complex stimulus processing and evaluation (Harper et al., 2014, 2016; Bernat et al., 2015; Watts et al., 2017), similar to distinctions inferred from work investigating P3a and P3b as detailed above.

1.4. Study goals & motivation

Evidence across several decades of research suggests a direct relationship between centroparietal delta and frontocentral theta activity to the P3b. This idea converges with Polich's modern interpretation of the P300 as a mixture of a frontocentral and centroparietal subcomponent, each reflecting different aspects of stimulus processing (Polich, 2007). The cumulative weight of this evidence suggests that studying delta and theta activity, rather than the time-domain P3b, may be useful in untangling the numerous functions underlying this large global process. Within this study we hope to not only reaffirm this relationship but also expand upon it in several domains. First, the majority of P3b studies noted above were conducted using auditory stimuli; therefore, a common goal across each of our five tests will be to show similar relationships between delta and theta activity to the visual oddball P3b as well. Second, this body of research was spread over the course of several decades, which saw the development and application of several different methodological approaches, such as different time-frequency transforms. These differences can impact how frequency activity is extracted and represented. By using the same methodological approach across several aims we will generate a comparable set of results using the same methodological procedure.

The study is designed to assess for the contributions of theta and delta to the P3b. This is first assessed with regard to shared versus unique variance (using regression analysis) in the P3b. While several studies have shown the presence of both oscillatory components underlying this ERP, very few have assessed their relative statistical contributions, an approach we have used before for the P3b (Gilmore et al., 2010), no-go N2 (Harper et al., 2014, 2016) and the FN (Bernat et al., 2011). This approach can provide an assessment of the degree to which theta and delta activity index separable processes, relative to a singular process. Next we tested how delta and theta change in activity as a function of changes in P3b activity, i.e. related to experimental manipulations and performance. The goal of these analyses was to test the degree to which these factors show unique contributions from theta and delta. To address this, we first replicate and extend widely studied manipulations (targets, non-targets, and target- non-target comparisons), and then apply this framework to understand target-to-target interval and target habituation, the latter of which has evidenced conflicting findings in the literature. Finally, we suggest that recent replication controversies motivate periodically re-testing ideas, particularly when there may be merit in applying new techniques, and with

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