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Prestimulus delta and theta determinants of ERP responses in the Go/NoGo task

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ABSTRACT

Ongoing low-frequency EEG activity has long been associated with ERP components and their cognitive processing interpretations, yet few studies have directly investigated the prestimulus low-frequency EEG–ERP relationships, particularly within the auditory domain. The present study assessed the delta (1–3 Hz) and theta (4–7 Hz) bands individually, and their prestimulus influence on five subsequent components (P1, N1, P2, N2, and P3) within an equiprobable auditory Go/NoGo paradigm. At the nine central sites, accepted trials were sorted according to their ascending vertex prestimulus spectral band amplitude, and ERPs were derived from the upper and lower sorted thirds. The within-subjects analyses included amplitudes and latencies for both Go and NoGo responses, and Go response speed. Only component amplitudes showed effects of high/low prestimulus EEG level. Delta globally modulated the five components — all amplitudes were more positive with high prestimulus delta, regardless of stimulus condition. Theta did not influence P1, but inversely modulated P2 and P3 regionally, and produced stimulus-specific effects in N1, N2, and P3. Low prestimulus theta produced greater NoGo N2 and Go P3, and reduced NoGo P3 responses, each of these suggesting appropriately enhanced cognitive processing. Taken together, these effect patterns differentially implicate prestimulus delta and theta band activity in the determination of ERP component amplitudes and the cognitive processing associated with them.

1. Introduction

When presented with a stimulus, there is a robust association between our ongoing electroencephalographic (EEG) activity and the amplitude and latency of the event-related potential (ERP) elicited. Across a range of auditory tasks (our focus here), two analytic approaches have consistently shown links between the poststimulus EEG activity of the low-frequency bands, here referring to delta (~0.5–3.5 Hz) and/or theta (~3.5–7 Hz), and the concomitant ERP components. Spectral analysis of the wide-band ERPs has shown dominant poststimulus amplitude/power contributions from one or both of these low-frequency bands (Başar et al., 1984; Başar-Eroglu et al., 1992, 2001; Başar-Eroglu and Demiralp, 2001; Spencer and Polich, 1999), particularly within the latency window of the endogenous components (>~250 ms). Coinciding peak characteristics are noted between the event-related oscillations (EROs: the poststimulus phase-locked EEG activity within a set band, typically derived via filtering) of the delta and/or theta band and the P3 (Başar and Stampfer, 1985; Karakaş et al., 2000; Stampfer and Başar, 1985; Yordanova and Kolev, 1998), amongst other components. Also, N1 and N2 amplitudes are topographically enhanced where delta EROs are minimal, and theta EROs are maximal (Barry, 2009).

Like the endogenous ERP components themselves, poststimulus activity in the delta and theta bands appears sensitive to stimulus and/or paradigm manipulation. For instance, in comparison to equiprobable Go stimuli, NoGo stimuli provoke greater and prolonged poststimulus spectral power enhancement in the low-frequency bands, particularly within the endogenous period (Barry, 2009). For oddball targets vs. nontargets, EROs amplitudes are enhanced in the delta and theta bands, the delta EROs peak is delayed, and the theta EROs amplitude enhancement is sustained (Stampfer and Başar, 1985). With increased task complexity, poststimulus increases are noted in the spectral amplitudes of the wide-band ERPs, and also in the EROs amplitudes, with these effects occurring across the broad poststimulus period for delta, and the endogenous-specific period for theta (Başar-Eroglu et al., 1992, 2001; Başar-Eroglu and Demiralp, 2001). Prolonged enhancement of the EROs in theta has also been reported for task compared to no-task conditions (Kolev and Schürmann, 1992). Parallel increases in low-frequency spectral power and P3 amplitudes have been reported with manipulations of stimulus repetition, probability, and response requirements (Spencer and Polich, 1999). Similarly, theta EROs and P3 amplitudes have shown simultaneous increases for oddball targets requiring a response, when compared to passive task conditions (Yordanova and Kolev, 1998).

The superposition of EROs across various bands, predominantly those of the low frequencies, was proposed to closely approximate the ERP (Başar and Stampfer, 1985; Stampfer and Başar, 1985). This has been supported, with EROs in the delta and theta bands reported to directly predict the N2 and P3 component amplitudes, accounting for 57–97% of their variation at midline sites across a range of paradigms (Karakaş et al., 2000). Moreover, a direct correlation has been

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found between single trial endogenous theta EROs and P3 amplitudes (Yordanova and Kolev, 1998), and as mentioned earlier, the topographies of the delta and theta EROs largely determine the N1 and N2 amplitude topographies (Barry, 2009). Overall, poststimulus EEG activity in the low-frequency bands appears to be closely related to ERP component characteristics.

Early investigations by Başar and colleagues also noted the occurrence of prestimulus spectral amplitude — EROs enhancements in the delta band following stimulation (Stampfer and Başar, 1985), and in the theta band for omitted stimuli (Başar et al., 1984) in some trials. These studies were exploratory, with no statistical analyses reported, and methodological concerns have been raised regarding their digital filtering (Barry et al., 2000). However, pre-post stimulus EEG spectral power increases in one or both low-frequency bands have since been confirmed using improved signal processing techniques including Fast Fourier Transform (FFT) algorithms (Barry, 2009; Yordanova and Kolev, 1998). Direct correlations have also been noted between prestimulus spectral amplitudes and poststimulus EROs amplitudes in the theta band at the single trial level (Yordanova and Kolev, 1998). Thus the low-frequency EEG activity outside the poststimulus period is considered to contribute to the ERP. For instance, the low-frequency spectral power of the 'background' EEG, recorded separately either before or after the ERP paradigm, is directly correlated with the size of the N1 for both target and standard oddball stimuli (Intriligator and Polich, 1995), and with target oddball P3 amplitude (Intriligator and Polich, 1994, 1995; Polich, 1997), when both the EEG and ERPs are recorded with open eyes. This 'background' EEG–P3 correlation has been consistent across a range of target probabilities (Intriligator and Polich, 1994), and across a broad age range (Polich, 1997). However, given the dynamic nature of the ongoing EEG fluctuations, we suggest that this non-task period is suboptimal to elucidate the most influential EEG determinants of the ERP — rather, the EEG brain state immediately preceding stimulus onset would seem more salient.

There remains some debate surrounding the underlying mechanism(s) involved in ERP generation, specifically the nature and extent of the EEG–ERP contribution. Of the two major models of ERP genesis, the evoked model describes the ERP as the sum of distinct event induced activity overlaying, and independent of, the ongoing EEG following stimulus onset (Barry, 2009; Jervis et al., 1983; Klimesch et al., 2007; Min et al., 2007; Sauseng et al., 2007). Alternatively, the phase-reset model implicates the phase spectra of the ongoing EEG as a determining factor in ERP genesis — that is, event-specific phase reorganization and alignment occur in specific frequencies of the ongoing EEG following stimulus onset (Barry, 2009; Klimesch et al., 2007; Min et al., 2007; Sauseng et al., 2007). Each model provides a differential account of the EEG–ERP relationship, but implicit within each model is the influence of the EEG activity immediately prestimulus (Min et al., 2007). We are not primarily concerned here with the mechanisms underlying each model; instead our interest is in their empirically assessable expression.

Remarkably few studies in the auditory domain have assessed the within-task prestimulus EEG–ERP relationships for the low-frequency bands. Rahn and Başar (1993) reported within-subject N1-P2 amplitude enhancements for low prestimulus theta trials. However, each stimulus presentation was contingent upon the spectral amplitude within each participant's theta band, and the possibility of biofeedback-type confounds has since been raised (Barry et al., 2000). Romani et al. (1988) found within-subject lengthening of N1 latencies across four ERPs derived from trials with increasing proportions of prestimulus combined delta and theta activity. Across these levels, participants with greater prestimulus low-frequency spectral amplitudes showed lower N1-P2 amplitudes and greater N1 latencies. The above two studies employed single-stimulus paradigms, the first a passive task, and the second a slow count task, providing only limited generalisability. Since then, Lazzaro et al. (2001) have reported increased oddball P2 amplitude, N1 and P3 latencies, and reaction time (RT), and decreased N2 amplitudes in an adolescent AD/HD population, who also had increased prestimulus spectral power within the theta band, compared to age- and sex-matched controls. Taken together, the findings across the three studies implicate prestimulus EEG activity in the delta and theta bands as important determinants of the N1, P2, N2, and P3 components and response performance, yet they remain to be systematically verified and extended to incorporate additional stimulus and task conditions.

In addition to the AD/HD field, low-frequency EEG and ERP covariations are mentioned in diverse literatures. From childhood to adolescence, developmental studies generally report reductions in delta and theta band power (Barry and Clarke, 2009), latency decreases for one or more of the N1, N2 and/or P3 components (Kolev et al., 2001), amplitude reductions in the NoGo N2, and increases in the P3 (Segalowitz et al., 2010). Delta band activity typically has limited and mixed findings within the meditation literature, although increases in theta power across differing meditation types, particularly transcendental, are generally noted, as is evidence for meditation-based P3 latency decreases (Cahn and Polich, 2006). Such covariations across literatures have prompted cognitive-processing interpretations of the functional significance of the low-frequency EEG bands, theta more so than delta.

Activity in the delta band has been associated with decision-making, signal detection, and/or stimulus matching, primarily due to the nature of its EROs amplitude enhancements with increased task complexity across paradigms (Başar et al., 2000, 2001; Başar-Eroglu et al., 1992, 2001; Başar-Eroglu and Demiralp, 2001). Theta has been implicated in several cognitive processes, most notably in relation to attention, due to its pattern of prolonged and/or endogenous EROs amplitude enhancement with increased task complexity across paradigms (Başar et al., 2000, 2001; Başar-Eroglu et al., 1992, 2001; Başar-Eroglu and Demiralp, 2001); as well as memory (Klimesch et al., 2007), with reduced prestimulus, and augmented poststimulus, spectral power in theta differentiating good from poor memory task performers (Klimesch, 1999). Moreover, the combined low-frequency EEG contributions to working memory appear important, given the selectively distributed nature of the EROs response across bands (Başar et al., 2000, 2001).

Our study aimed to investigate the nature and extent of the prestimulus delta and theta determinants of five ERP components (P1, N1, P2, N2, and P3) in an equiprobable auditory Go/NoGo paradigm. This task was selected to decrease stimulus probability and inhibition-related confounds (Lavric et al., 2004). We decided to assess the spectral amplitude of the prestimulus EEG at the vertex as this is the centre of the nine scalp sites where ERPs were to be examined. For each EEG band, two levels of within-subject prestimulus activity (high vs. low) were used to investigate amplitude and latency effects in each ERP component and stimulus condition separately. Go RT was also included, allowing the assessment of prestimulus low-frequency EEG effects on behavioural performance. No formal hypotheses were made for either band across the measured outcomes, although speculations were extrapolated from the limited reports reviewed above. Given Romani et al.'s (1988) findings, prestimulus delta activity might directly modulate N1 latency, and inversely modulate N1 and P2 amplitudes. As their study employed a slow counting task, it was uncertain what effect prestimulus delta would have on RT performance, if any at all. Prestimulus theta may show a direct association with the component latencies of the N1 (Romani et al., 1988), and perhaps also P2, N2, and P3 (Lazzaro et al., 2001). Despite conflicting evidence reported for P2 (Lazzaro et al., 2001), N1 and P2 amplitudes might be inversely modulated by prestimulus theta — the more common finding (Rahn and Başar, 1993; Romani et al., 1988). Prestimulus theta may also be inversely associated with N2 amplitudes, and directly with RT performance (Lazzaro et al., 2001). No predictions were made for either band regarding the P1 component, which does not appear to have been