

Journal Code: PSYP	Proofreader: Mony
Article No: PSYP12210	Delivery date: 17 Mar 2014
Page Extent: 15	

Psychophysiology, •• (2014), ••–••. Wiley Periodicals, Inc. Printed in the USA.
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DOI: 10.1111/psyp.12210

EEG delta oscillations index inhibitory control of contextual novelty to both irrelevant distracters and relevant task-switch cues

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Abstract

Delta oscillations contribute to the human P300 event-related potential evoked by oddball targets, although it is unclear whether they index contextual novelty (event oddballness, novelty P3, nP3), or target-related processes (event targetness, target P3b). To examine this question, the electroencephalogram (EEG) was recorded during a cued task-switching version of the Wisconsin card-sorting test. Each target card was announced by a tone cueing either to switch or repeat the task. Novel sound distracters were interspersed among trials. Time-frequency EEG analyses revealed bursts of delta (2–4 Hz) power associated with enhanced nP3 amplitudes to both task-switch cues and novel distracters—but no association with target P3b. These findings indicate that the P300-delta response indexes contextual novelty regardless of whether novelty emanates from endogenous (new task rules) or exogenous (novel distracters) sources of information.

Descriptors: Cognitive control, Novelty P3, Task switching

Contextually novel events that capture attention away from an ongoing task also elicit a brain potential referred to as the “novelty P3” (Escera, Alho, Schröger, & Winkler, 2000; Escera, Alho, Winkler, & Naatanen, 1998; Friedman, Cycowicz, & Gaeta, 2001; Ranganath & Rainier, 2003). The novelty P3 (nP3) is often taken to indicate that a novel, unexpected distracter has captured attention away and, at that point in time, is most likely within the focus of mind (Escera, Yago, & Alho, 2001; Friedman et al., 2001). Paradoxically, familiar and repetitive contextual cues that announce an intentional switch to new task rules also elicit nP3 responses and activate a network of brain regions akin to that implicated in the processing of task-irrelevant novel distracters, an original idea referred to as the “task novelty hypothesis” (Barcelo, Escera, Corral, & Perianez, 2006; Barcelo, Perianez, & Knight, 2002). In these studies, the morphology, latency, and frontal-central scalp distribution of brain nP3 responses to task-switch cues were comparable to the morphology, latency, and frontal-central distribution of brain nP3 responses to novel distracters. Hence, the task novelty hypothesis reconciles two seemingly paradoxical findings by proposing that task-novelty and stimulus-novelty both activate a

common network of corticosubcortical regions involved in processing contextual novelty (Barcelo et al., 2002, 2006). The main aim of this study was to address the task-novelty hypothesis from a time-frequency approach, in order to clarify which of the two aspects of the endogenous P300 component of the human event-related potential (ERP) typically elicited in novelty oddball paradigms, either the distracter-locked novelty P3 (nP3) or the target-locked P3b, best corresponds with the well-known P300-delta response described in the literature (Basar-Eroglu, Basar, Demiralp, & Schürmann, 1992; Basar-Eroglu, Demiralp, Schürmann, & Basar, 2001; Demiralp, Ademoglu, I Stefanopulos, Basar-Eroglu, & Basar, 2001; Demiralp, Ademoglu, Schürmann, Basar-Eroglu, & Basar, 1999; Mathes, Schmiedt, Schmiedt-Fehr, Pantelis, & Basar-Eroglu, 2012; Schürmann, Basar-Eroglu, Kolev, & Basar, 1995; Schürmann, Basar-Eroglu, Kolev, & Basar, 2001; Yordanova, Devrim, Kolev, Ademoglu, & Demiralp, 2000; Yordanova & Kolev, 1998a, 1998b).

Time-frequency electroencephalogram (EEG) analyses have long revealed strong bursts of delta and theta EEG power that contribute to the elicitation of the endogenous P300 component (peak latency 300–500 ms poststimulus onset) to surprising and motivationally relevant target stimuli delivered in oddball paradigms (Basar-Eroglu et al., 1992; Demiralp et al., 1999; Schürmann et al., 1995; Yordanova et al., 2000; Yordanova & Kolev, 1998b). Most of these studies employed variants of the two-stimulus oddball paradigm and showed that the endogenous P300 component correlates with the delta (1–4 Hz) response to auditory targets involving signal matching to surprising or unexpected events (Basar-Eroglu et al., 1992; Demiralp et al., 1999). A

This work was supported by grants from Fundació La Marató TV3 (ref. 112710), the Generalitat de Catalunya (SGR2009-11), the Spanish Ministry of Science and Innovation (PSI2010-17419, Consolider-Ingenio 2010 CSD2007-00012), and an ICREA Academia Distinguished Professorship awarded to CE.

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few studies also employed three-stimulus novelty oddball tasks and showed that the delta response is also elicited by novel distracters, which was interpreted as an index of surprise during signal matching (Demiralp et al., 2001; Isler, Grieve, Czernochowski, Stark, & Friedman, 2008). In turn, concurrent bursts of theta power within the P300 latency range have been attributed to focused attention and signal detection. Thus, Basar-Eroglu et al. (1992) reported a prolongation of delta and theta oscillations in response to oddball targets. Significant increases in delta and theta power were recorded only in the late part of the ERP window (250–500 ms), and these power increases were widely distributed across frontal, central, and parietal locations. However, these early studies did not clarify whether the delta (and theta) power responses index selection of infrequent target stimuli, inhibition of infrequent distracter stimuli, or higher-order decision making about task rule selection.

Hence, one important question that awaits clarification is whether the P300-delta response to oddball targets reflects the neural processing of infrequent, surprising, and unexpected stimuli (i.e., event oddballness, novelty P3), or else the processing of motivationally relevant target stimuli (i.e., event targetness, target P3b). This is an important question since the oddballness and targetness aspects likely involve different neural processes each related to distinct task preparation and task execution mechanisms, respectively (Barcelo & Knight, 2007), which cannot be easily dissociated in the canonical P300 to oddball targets (Donchin, 1981). In fact, the brain responses measured in classic oddball paradigms likely confound the preparatory resolution of stimulus uncertainty (oddballness, nP3) with task execution processes (targetness, target P3b) such as the selection and implementation of a motor response (cf. Barcelo et al., 2006; Barcelo & Knight, 2007). Arguably, detection of an oddball target requires not only an infrequent updating of its sensory representation in working memory, but also the updating of the equally infrequent motor program for response execution (Mars et al., 2008). This functional multiplicity of the target P3b evoked by oddball targets has been addressed using independent component analyses (ICA; Makeig et al., 1999). Likewise, cued task-switching paradigms provide a means for isolating these two distinct types of P300 activations related to two distinct and temporally ordered stages in the top-down control of behavior (Adrover-Roig & Barcelo, 2010; Perianez & Barcelo, 2009). Task cues usually predict target onset at fixed intervals, and, hence, cue-locked ERPs offer a measure of event oddballness (i.e., cue novelty, contextual surprise) uncontaminated from target processes. Likewise, target-locked ERPs offer a purer measure of target processing (i.e., stimulus evaluation, response selection, etc.) uncontaminated from event oddballness. Task-cuing paradigms are well suited to clarify whether the delta response to oddball targets indexes either the oddballness or the targetness of the eliciting events, as the corresponding neurophysiological signatures (nP3 vs. target P3b) are known to reflect distinct cognitive operations subserved by different anatomical substrates (Barcelo & Knight, 2007; Ranganath & Rainier, 2003).

To date, few studies have applied time-frequency analyses of brain oscillations to investigate the neural dynamics of cognitive control during task switching, and none of them explored the low frequencies present in the delta response (cf. Cunillera et al., 2012; Gladwin & de Jong, 2005; Gladwin, Lindsen, & de Jong, 2006; Mansfield, Karayanidis, & Cohen, 2012; Sauseng et al., 2006; Verstraeten & Cluydts, 2002). For instance, Verstraeten and Cluydts (2002) found that efficient task-switching performance was associated with low (8–10 Hz) alpha suppression, whereas

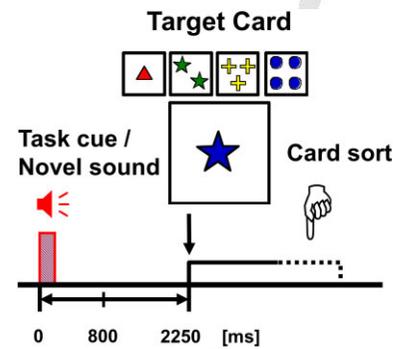


Figure 1. Schematic example of one trial of the task-cueing protocol. Tonal “switch” cues signalled a change in the task rule, whereas tonal “repeat” cues prompted the subject to repeat the previous task rule. The pitch of switch and repeat cues was counterbalanced across subjects (500 and 1000 Hz, or vice versa). The target card remained on display until a button response was given. Novel sound distracters were randomly interspersed in one of two blocks of trials (200-ms duration; 10-ms rise/fall times; 75 dB SPL for all auditory stimuli).

power increases in the high alpha (10–12 Hz) range indexed inaccurate attentional set switching. Gladwin and de Jong (2005) reported distinct modulations of theta and alpha oscillations during the preparation and execution stages of task switching, and found increases in theta power accompanied by alpha decreases over occipital regions while subjects prepared to alternate tasks relative to when repeating the same task. Gladwin et al. (2006) further demonstrated significant changes in the theta, alpha, and beta bands between task preparation and execution stages in an alternating-runs paradigm, some of which matched the speed and accuracy of behavioral responses. Likewise, Sauseng et al. (2006) found stronger long-range theta coupling between prefrontal and posterior scalp regions during switch as compared to repeat trials as an index of top-down cognitive control. Actually, none of these earlier studies employed a task-cueing paradigm for disentangling the relative contribution from task preparation and task execution stages in the top-down control of behavior. More recently, Cunillera et al. (2012) reported significant increases in theta power accompanying sizeable frontal-central nP3-like potentials following both a switch cue as well as the first positive feedback after a task switch. Mansfield et al. (2012) also reported evidence within the alpha band for dissociable early switch-related preparation and later task readiness across frontal and parietal cortical regions, respectively. However, the main effects of these two studies were confined within the theta and alpha bands, respectively, and none reported modulations within the delta band.

The present study aimed to extend previous ERP findings by exploring the oscillatory basis of the cue-locked nP3 component observed in a cued task-switching paradigm inspired in the Wisconsin card sorting test (WCST). Following the original procedures, ERPs were recorded while subjects sorted cards using one of two rules of action (color or shape of items in the cards). Each card was preceded by a familiar tone cueing the subject either to switch or to repeat the previous rule. Novel sound distracters were interspersed in one of two blocks of trials (Figure 1). Our main objective was to reexamine the “task novelty” hypothesis that mental set switching to new tasks and novel distracters both recruit activity from a common network of brain regions by employing a time-frequency approach. Time-frequency analyses comprise many methods and measures that capture various aspects of EEG

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dynamics in terms of magnitude and phase relationships (Cohen, 2011). Here, we studied event-related spectral power changes (ERSP) and intertrial phase coherence (ITC; Makeig et al., 2002) of brain rhythms involved in the generation of P300 potentials evoked by tonal task cues, visual targets, and novel distracters. It was hypothesized that, if task-nP3 shares a common neural substrate with stimulus-nP3, and the delta response is associated with the elicitation of nP3 potentials during mental set switching, then both novel distracters and task-switch cues should elicit similar delta power changes within the P3 latency range. On the contrary, no delta power changes were predicted for target P3b responses in correct switch trials, as these were assumed to reflect a different mechanism related to the efficient exploitation of the task-set information available in working memory (Barcelo et al., 2002, 2006).

Method

Participants

Twelve young subjects (mean age 21 ± 0.5 years, range 19–24 years; 7 women) took part in the study. All participants had normal or corrected-to-normal vision and reported no history of neurological or psychiatric disorders. The experiments were performed in accordance with the Declaration of Helsinki, and informed consent was obtained from all subjects.

Stimuli and Procedure

The task protocol consisted of a computerized version of a cued task-switching protocol inspired by the WCST (Rubinstein, Meyer, & Evans, 2001), and adapted for measuring ERPs (Barcelo, 2003). Each trial consisted of a tonal cue followed by a target display with four key cards on top of one choice card, all centered on a computer screen 2 m from the observer (Figure 1). The target stimulus subtended a visual angle of $3.5^\circ \times 3.5^\circ$, and remained on display until a response was given. Subjects were instructed to match the choice card with one of the four key cards following two rules (color or shape of items in the card). Subjects were told that the correct rule would randomly change on a trial-by-trial basis, and they should shift their sorting rule accordingly. Before target onset, a tonal cue informed the subject whether to switch or repeat the previous task (200-ms duration, 10-ms rise/fall times; 75 dB SPL; 500 Hz and 1000 Hz binaural tones for “switch” and “repeat” cues, respectively; the tone-to-cue mapping was reversed for half the subjects). Tonal switch and repeat cues occurred unpredictably with the same overall probability ($p = .5$). Subjects used their thumbs for responding while holding a four-button response panel in their palms. The far left button designated the key card on the far left of the display, the far right button designated the key card on the far right, and so on. Response-to-cue intervals varied randomly between 800 and 1,500 ms, with a constant cue-to-target onset asynchrony of 2,250 ms (Figure 1). This task-cueing paradigm allowed us to segregate neural activity related to cue-locked (task preparation) and target-locked (task implementation) processes (Adrover-Roig & Barcelo, 2010; Barcelo, 2003; Perianez & Barcelo, 2009; Rubinstein et al., 2001).

Prior to the experimental run, subjects were fully instructed about the task rules, and received practice for 5–10 min until they reached a criterion of 100% correct sorts during 1 min. Wrong feedback was delivered following wrong responses during both practice trials and the experimental runs. Each subject completed two blocks of 140 trials, with a 10-min rest period between blocks.

Overall accuracy was better than 85% correct trials in all subjects. Twenty-six trials with nonidentifiable novel sounds were randomly interspersed in one of the two blocks. Novel sounds appeared randomly between 700 and 1,100 ms after a task-repeat cue while keeping a constant novel-to-target stimulus onset asynchrony of 2,250 ms as in all other trials (Figure 1). Novel sounds were not presented during the practice sessions, and each sound was used only once in the whole study. Task-repeat trials containing a novel sound were used to compute “stimulus-nP3” waveforms, but were excluded from the computations of the cue-locked and target-locked ERP averages. The order of presentation of the trial block containing novel sound distracters was counterbalanced across subjects.

EEG Acquisition

The EEG was recorded from 28 tin electrodes positioned at Fp1, Fp2, F7, F3, Fz, F4, F8, FC1, FT3, FT4, T5, T3, C3, Cz, C4, T4, T6, P3, Pz, P4, TP3, CP1, CP2, TP4, M2, O1, and O2, and referenced to the left mastoid. The EEG signal was amplified (band-pass, 1–30 Hz; 12 dB/octave roll/off), digitized at 500 Hz/channel and stored for offline averaging. Electrode impedances were kept below 5 k Ω . The electrooculogram (EOG) was recorded for eye blink correction and rejection of other eye movement artifacts.

ERP Analyses

All epochs were visually inspected for artifacts, and epochs containing uncorrected eye movements were rejected using ICA (Delorme & Makeig, 2004). In addition, epochs with EEG exceeding $\pm 60 \mu\text{V}$ in amplitude were discarded. ERPs were computed as mean amplitude averages in microvolts across all trials in a time window ranging from 200 ms before stimulation to 1,000 ms after stimulus onset. They were corrected for baseline activity that occurred in the 200 ms before stimulation. The peak latency of endogenous P300 potentials are proportional to stimulus evaluation timing, are sensitive to task processing demands, and vary with individual differences in cognitive capability. Therefore, different time windows were set for the measurement of mean nP3 and target P3b amplitudes. Mean nP3 amplitudes were computed across participants over a 100-ms window centered on the peak latency of the nP3 component: 350 ms for cue-locked ERPs (time window 300–400 ms poststimulus onset), thus yielding one grand average for each task condition (task-repeat cue, task-switch cue, novel sound). Measurement of mean nP3 amplitudes was also applied to the target-locked ERPs as a control. Target-locked P3b amplitudes (400–600 ms post-target onset) were computed to examine the implications of the experimental manipulations for the context updating model of the P300 component (Donchin, 1981). In order to maximize the differences between the brain responses to switch and repeat trials, the first repeat cue following a switch cue was not considered in these analyses, as first repeat cues have been shown to elicit residual nP3 activity (Barcelo, 2003; Barcelo et al., 2002). Likewise, mean values for ERSP and ITC in the same latency windows were also calculated for each subject as described below.

Time-Frequency Analyses: Wavelets

For nonstationary EEG signals, time-frequency analyses provide information about which oscillations dominate at any moment in time. Wavelet analyses offer the best compromise between temporal and frequency parameters. The wavelet transform is a

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Table 1. Wavelet Parameters Responsible for Temporal and Spectral Resolution

	3 Hz frequency	
	Spectral resolution (Hz)	Temporal resolution (ms)
Wavelet _{n=1}		
Wavelet duration = 7σ _t	2σ _f = 6	2σ _t = 106
Wavelet _{n=6}		
Wavelet duration = 7σ _t	2σ _f = 1	2σ _t = 636

multiresolution analysis technique that splits up the signal into different frequency components, in order to examine each spectral component with a time resolution matched to its frequency (Demiralp et al., 1999). The time-frequency analysis was done with a Morlet wavelet decomposition using the EEGLAB toolbox (Delorme & Makeig, 2004), under MATLAB 7.0 (The Mathworks, Inc.). The Morlet function has a Gaussian distribution both in the time and frequency domains. Its standard deviation in the time domain is given by $\sigma_t = (2\pi\sigma_f)^{-1}$ and in the frequency domain is defined by a constant ratio $\sigma_f = f/n_c$, where n_c is a constant number and f is the center frequency. If n_c is constant, σ_f grows proportionally to the modulation frequency, which means different time and frequency resolution ($2\sigma_t$, $2\sigma_f$) at different frequencies. Therefore, for progressively higher frequency components of EEG signals, the Morlet function gives a good temporal resolution, whereas its frequency resolution decreases correspondingly. Conversely, for the low-frequency components, it leads to a good frequency resolution at the expense of a comparatively reduced time resolution. By adapting the window size of the wavelet along the temporal dimension as a function of the (high or low) frequency component of interest, wavelet analysis offers a good compromise for time-frequency resolution, which has been critical for its success and extended use in EEG signal analysis. The amplitude of the wavelet transform used provides energy units at all scales:

$$A\psi = \sigma_t^{-1/2} \cdot \pi^{-1/4} \quad (1)$$

For a more in-depth description of wavelets and their application to EEG signal analyses, several excellent reviews are available (cf. Herrmann, Busch, & Grigutsch, 2005). In order to make an optimal interpretation of wavelet analyses of the P300 component, oscillatory EEG activity was analyzed using two different wavelets: The first wavelet (wavelet_{n=1}) provided an optimal temporal resolution at low frequencies for detecting the nP3 and target P3b components in time. The second wavelet (wavelet_{n=6}) offered an optimal frequency resolution at low frequencies to better identify the frequency decomposition of the P300 component (see Table 1). Two parameters were derived from the wavelet-transformed data: the ERSP and the ITC.

The **event-related spectral perturbation** shows average dynamic changes in the amplitude of the EEG frequency spectrum as a function of time:

$$ERSP(f, t) = \frac{1}{n} \sum_{k=1}^n (F_k(f, t))^2 \quad (2)$$

where for n trials, $F_k(f, t)$ is the spectral estimate of trial k at frequency f and time t . The ERSP index estimated changes in

spectral power from a 400-ms baseline extending from -500 to -100 ms before stimulus onset, and across a frequency range 2–30 Hz. The wavelet transform was computed for each individual trial, and the values obtained were averaged. These values are expressed in decibels (dB) and reflect the total activity (compared to baseline) independently of whether it is phase-locked to the stimulus or not. Therefore, this measure comprises two major sources of event-related oscillatory activity: evoked activity (phase-locked) and induced activity (nonphase-locked).

The **phase locking factor** was computed with the event-related intertrial coherence index, which shows the consistency across trials of EEG spectral phase at each frequency and latency window (Makeig et al., 2002):

$$ITC(f, t) = \frac{1}{n} \left| \sum_{k=1}^n \frac{F_k(f, t)}{|F_k(f, t)|} \right| \quad (3)$$

where $||$ represents the complex norm (Delorme & Makeig, 2004). ITC adopts values from 0 to 1 that point out the synchronized phase across trials with respect to event onset. The value 0 implies a uniformly scattered phase across all trials, and the value 1 implies perfect phase coherence across all trials. The phase-locking factor is an important complement to the total power because the values on which power calculations depend have no influence on the phase angles used to compute the phase-locking factor. In order to compare ERSP and ITC across task conditions, the number of trials for each condition was adjusted to be the same, to guarantee that our results could not be attributed to an effect of the size of the samples.

Statistical Analyses

The statistical analysis of ERPs and frequency band activity was performed on regional means to avoid loss of statistical power. By averaging across electrodes placed along the anterior-posterior axis, channels were pooled into three regions of interest (ROIs; frontal: F3, Fz, F4; central: C3, Cz, C4; posterior: P3, Pz, P4). These electrode sites showed the highest values of amplitude for the nP3 and target P3b components as conventionally used in P300 studies. A two-way repeated measures analysis of variance (ANOVA), with auditory event (switch cues, repeat cues, and novel sounds) and the three ROIs as factors, was used to test the task-novelty hypothesis. Another ANOVA design focused on brain responses to the target stimuli following each auditory cueing event, with cueing event (switch and repeat) and the three ROIs as factors. This second ANOVA examined whether predictions from the task-novelty hypothesis held merely for cue-locked nP3, or also for target-locked P3b amplitudes, and their corresponding oscillatory brain responses. Statistical significance for within-subject factors were computed using the Greenhouse-Geisser correction (Jennings, 1987). All post hoc tests of simple effects were performed using the Bonferroni correction with a significance level of $p < .05$. These ANOVA designs were carried out on mean cue-locked nP3 and target-locked P3b amplitudes, as well as on mean ITC and ERSP values extracted for each of the three frequency bands of interest (delta: 2–4 Hz; theta: ~4–8 Hz; alpha: ~8–12 Hz). Most previous studies on the P300-delta response examined delta power within 1–4 Hz (Basar-Eroglu et al., 2001; Demiralp et al., 2001; Schmiadt-Fehr & Basar-Eroglu, 2011; Yordanova et al., 2000), although they typically found a “center frequency of 2 Hz in the frequency domain” (Basar-Eroglu et al., 1992, p. 167).

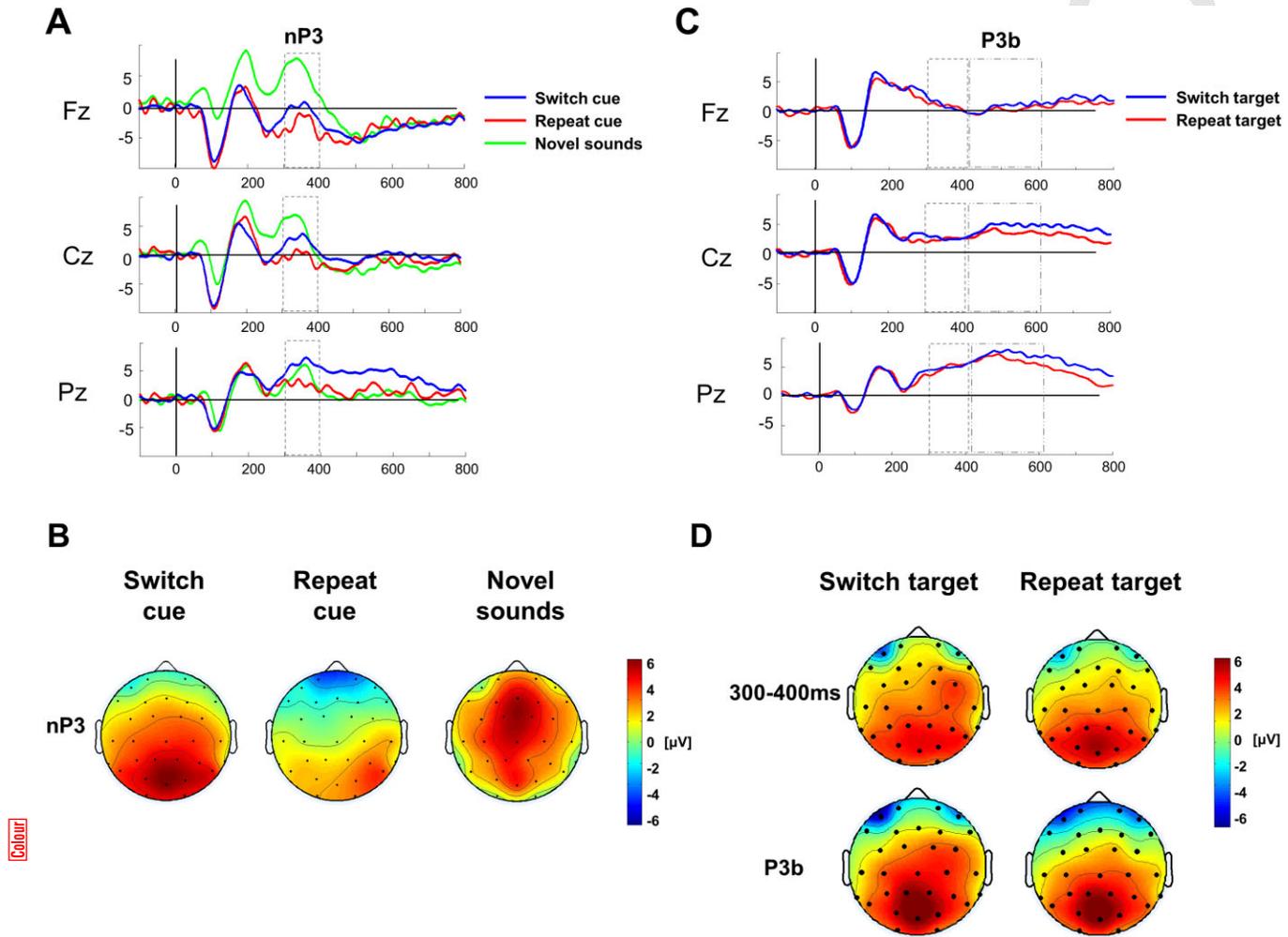


Figure 2. Grand-averaged ERPs and spline-interpolated scalp maps. A: Auditory ERPs displayed at three midline electrodes in response to task-switch cues, task-repeat cues, and novel sounds. B: Spline-interpolated scalp maps of mean nP3 voltages in response to switch cues, repeat cues, and novel sounds. The latency window for mean nP3 averaging was from 330–350 ms. C: Target-locked ERPs displayed at three midline electrodes in response to visual targets in task-switch and task-repeat trials. D: Spline-interpolated scalp maps of mean nP3 and target P3b voltages in response to task-switch and task-repeat visual targets. The latency window for mean ERP averaging was from 330–350 ms.

To study the relationship between different brain oscillations and mean P300 amplitudes, a series of linear regression analyses (R^2) were performed at the three ROIs using mean nP3 and P3b amplitudes as the criterion variable, with ERSP and ITC values as predictor variables. A statistically significant ($p < .05$) coefficient of determination, R^2 , was taken to indicate that mean P300 amplitudes were modulated by ERSP or/and ITC at the three frequency bands of interest. These regression analyses were performed using time-frequency values obtained from $\text{wavelet}_{\text{ic}=1}$, since these offer the best temporal resolution at low frequencies.

Results

ERPs

The grand-average ERPs and scalp topographies to tonal task cues, novel sounds, and visual target cards are presented in Figure 2. The grand-average stimulus-nP3 to novel sound distracters showed its usual peak latency (350 ms at Fz; Figure 2A) and frontal-central scalp distribution (Figure 2B), whereas task-switch and task-repeat

cues elicited task-nP3 potentials with a similar latency but with a more posterior scalp distribution than the stimulus-nP3 (Figure 2B; cf. Barcelo et al., 2006).

A main effect of auditory event, $F(2,22) = 4.34$, $p < .042$, and a significant interaction Auditory event \times ROI, $F(4,44) = 22.24$, $p < .0001$, were observed. A significant main ROI effect, $F(2,22) = 16.36$, $p < .01$, reflected the expected frontoparietal gradient (Fz < Cz < Pz) in the scalp distribution of nP3 amplitudes. Task-nP3 responses to tonal switch cues were comparatively smaller in amplitude than those evoked by novel sounds over frontal regions ($p < .1$), but not at central or more posterior regions ($F_s < 1$). Task-repeat cues elicited much reduced nP3 amplitudes over midline sites compared to both task-switch cues ($p < .01$) and novel sounds ($p < .01$).

Target-locked ERPs and scalp topographies to visual target cards in switch and repeat trials are shown in Figures 2C and 2D, respectively. Mean nP3 and P3b amplitudes to the visual targets were not sensitive to the manipulation of task novelty (with no differences in mean target P3b amplitude between switch versus repeat target trials; $F < 1$), a result consistent with previous studies

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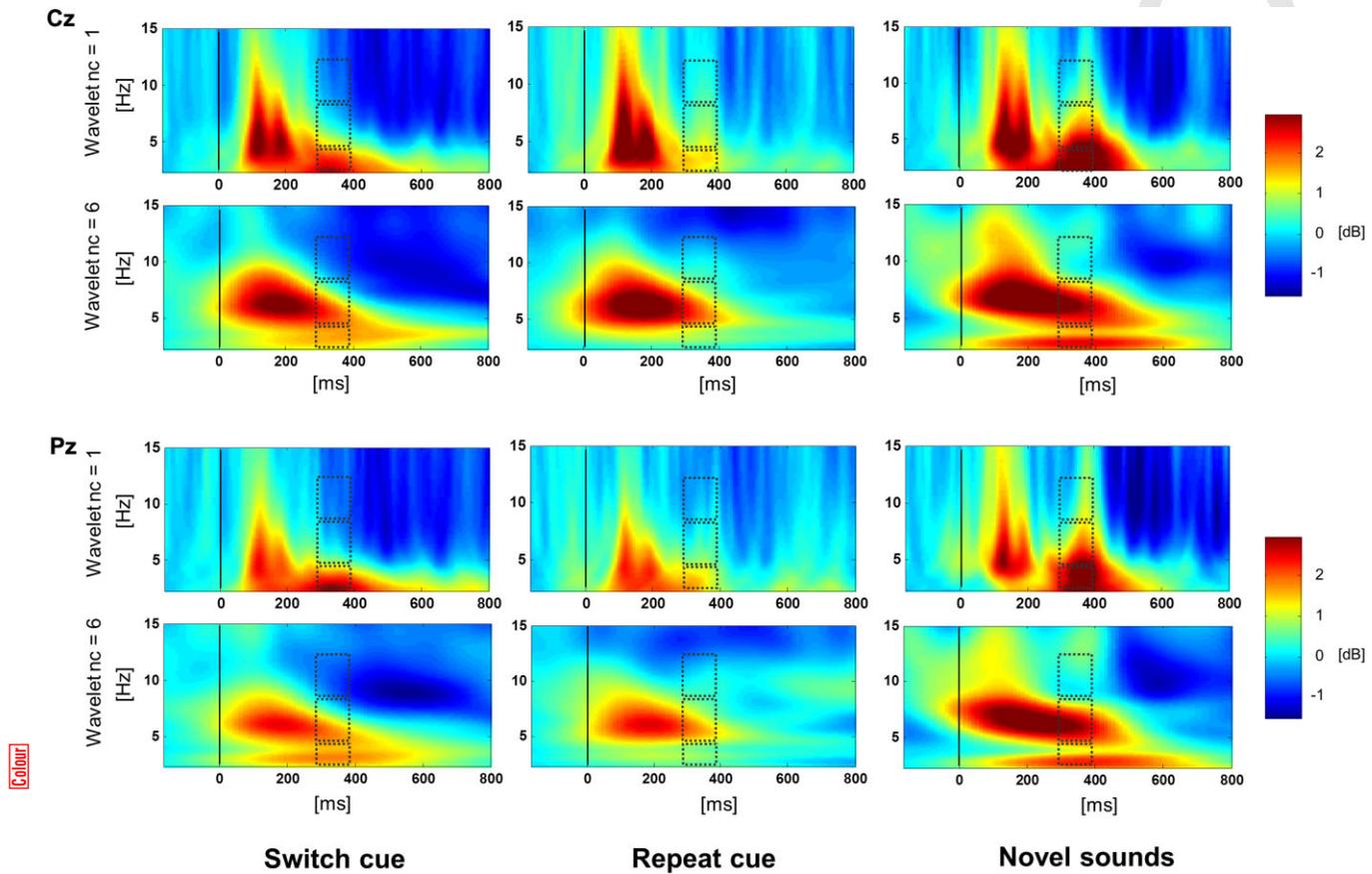


Figure 3. Event-related spectral perturbation (ERSP) in response to auditory events. ERSP plots for task-switch cues, task-repeat cues, and novel sounds at Cz and Pz electrodes for EEG frequencies ranging from 2.2–15 Hz. Two wavelet transforms were considered in the analyses: Wavelet_{nc=1}, offering optimal temporal resolution; and Wavelet_{nc=6}, offering optimal spectral resolution. Auditory stimuli occurred at 0 ms. The power level is coded on a color scale in decibels. The boxes indicate the time and frequency windows used in the statistical analyses to assess the contribution of alpha, theta, and delta oscillations (from top to bottom). Note that these boxes were tailored to the latency of nP3—not to the maximum of the plot.

that employed equiprobably interspersed switch and repeat trials (Barcelo et al., 2006; Gladwin & de Jong, 2005; Perianez & Barcelo, 2009).

ERSP

The results for ERSP values, reflecting changes in spectral power from baseline in response to the auditory task cues and novel sounds as well as to the visual targets, are shown in Figures 3 and 4, respectively. Each condition was analyzed using the previously defined wavelet_{nc=6} transform and, unless otherwise stated, we will primarily rely on the statistical results from wavelet_{nc=6} analyses offering an optimal spectral resolution to avoid any confound with theta oscillations. However, wavelet_{nc=6} analyses offer a poor temporal resolution (636 ms at a center frequency of 3 Hz, Table 1), with its frequency components shown as elongated blobs along the temporal scale, which may raise doubts about the true temporal origin of the observed P300-delta responses (as potentially related to earlier P1, N1, or later ERP components). Hence, to help interpret the temporal origin of the observed delta modulations, wavelet_{nc=1} analyses were also computed for an optimal temporal resolution (106 ms at 3 Hz center frequency; Table 1).

The ERSP for tonal task cues and novel sounds focused in the delta band for both wavelet analyses. The ANOVAs for delta ERSP

changes yielded significant main effects for auditory event, $F_s(2,22) > 5.63$; $p_s < .01$, which revealed significant delta ERSP changes evoked by both task-switch cues and novel sounds compared to task-repeat cues for both wavelet transforms. In contrast, no differences were apparent between task-switch cues and novel sounds. A marginally significant main effect of ROI, $F_s(2,22) > 3.19$; $p_s < .08$, reflected the typical $F_z < C_z < P_z$ scalp distribution also for ERSP values. A significant interaction between auditory event and ROI was found for delta ERSP computed with wavelet_{nc=6}, $F(4,44) = 3.1$, $p < .05$, suggesting different delta ERSP modulations across the three midline electrode regions, so that the effects of auditory event previously described were mostly found at central ($p < .05$) and parietal regions ($p < .05$) rather than at frontal regions (Figure 3; red blobs in the delta band 300–400 ms poststimulus). This increment in delta power in response to task-switch cues and novel sounds over central and parietal regions thus corresponds with the well-known P300-delta response (also see linear regression analyses below).

In the theta band, a marginally significant effect of auditory event was found using wavelet_{nc=6}, $F_s(2,22) = 2.6$; $p < .08$. Unlike in the delta range, there was a significant increment in theta power responses to novel sounds in comparison to both task-switch ($p < .01$) and task-repeat cues ($p < .05$). In contrast, no significant differences in theta power were elicited by switch and repeat cues.

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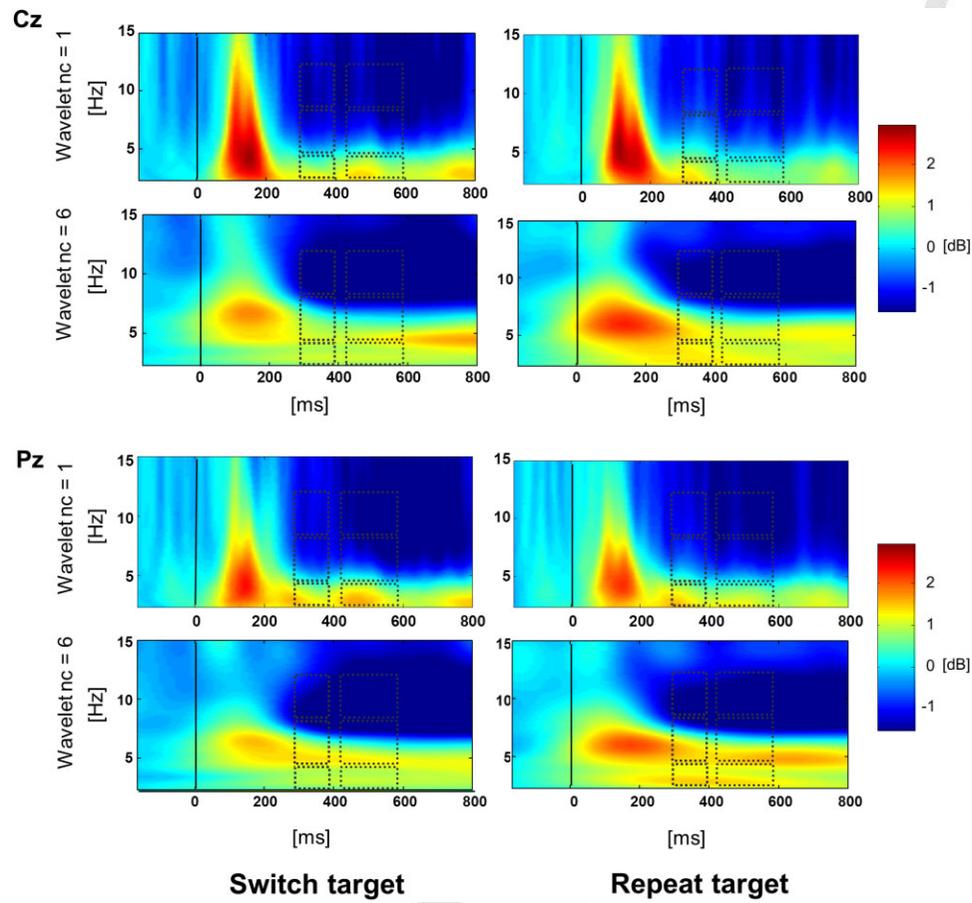


Figure 4. ERSP in response to visual targets. ERSP plots for visual targets in task-repeat and task-switch trials at Cz and Pz electrodes for EEG frequencies ranging from 2.2–15 Hz. Two wavelet transforms were considered in the analyses: $\text{Wavelet}_{nc=1}$, offering an optimal temporal resolution; and $\text{Wavelet}_{nc=6}$, offering an optimal spectral resolution. Target onset occurred at 0 ms. The power level is coded on a color scale in decibels. The boxes indicate the time and frequency windows used in the statistical analyses.

Finally, there were no main effects or interactions in the analyses of cue-locked ERSP within the alpha band (Figure 3).

For target-locked ERSP changes within the nP3 latency window, no main effects or interactions were observed in the delta or theta bands using $\text{wavelet}_{nc=1}$ and $\text{wavelet}_{nc=6}$ transforms (Figure 4). In turn, in the alpha band with $\text{wavelet}_{nc=1}$, visual targets in task-switch trials generated reduced alpha power compared to task-repeat targets, $F(1,11) = 5.18$; $p < .044$. Within the target P3b window, no main effects or interactions were observed for any of the wavelet transforms and frequency bands studied (Figure 4).

Figure 5 shows the temporal dynamics of ERSP to both tonal cues and novel sounds within the delta and theta frequency ranges at central and parietal regions, starting 200 ms before stimulus onset and up to 800 ms poststimulus onset. The significant effects observed at the nP3 latency window are marked with an asterisk. Within the delta band, there were significant differences in ERSP changes between task-switch cues and task-repeat cues, but not between task-switch cues and novel sounds at both central and parietal sites ($ps < .05$). Within the theta band, no ERSP differences were found between task-switch and task-repeat cues, although both types of cues evoked less theta power compared to novel sounds at both central and parietal regions ($ps < .05$; Figure 5).

Figure 6 illustrates the scalp topographies of ERSP to tonal cues and novel sounds within the delta frequency range. Enhanced delta power was observed in response to tonal task-switch cues at central and posterior electrodes, while novel sounds elicited a delta response with a wider frontoparietal scalp distribution. Noteworthy, these scalp topographies of enhanced delta power were comparable to the isovoltage scalp maps for cue-locked nP3 amplitudes (Figures 2B, 6).

ITC

For cue-locked ITC indexes, reflecting phase synchronization with respect to the onset of task cues and novel sounds, each auditory condition was analyzed using the two previously defined $\text{wavelet}_{nc=1}$ and $\text{wavelet}_{nc=6}$ (Figure 7). In the delta, theta, and alpha bands, and for both wavelet analyses, the ANOVAs yielded significant main effects of auditory event within the nP3 latency range, $F_s(2,22) > 5.92$; $ps < .013$. Looking at this effect, no significant differences were found between ITC indexes for switch and repeat cues, and both conditions showed significantly smaller ITC indexes than novel sounds ($ps < .01$). Neither the main ROI effect, nor the Auditory event \times ROI interaction reached significance. For target-locked ITC in the delta, theta, and alpha bands,

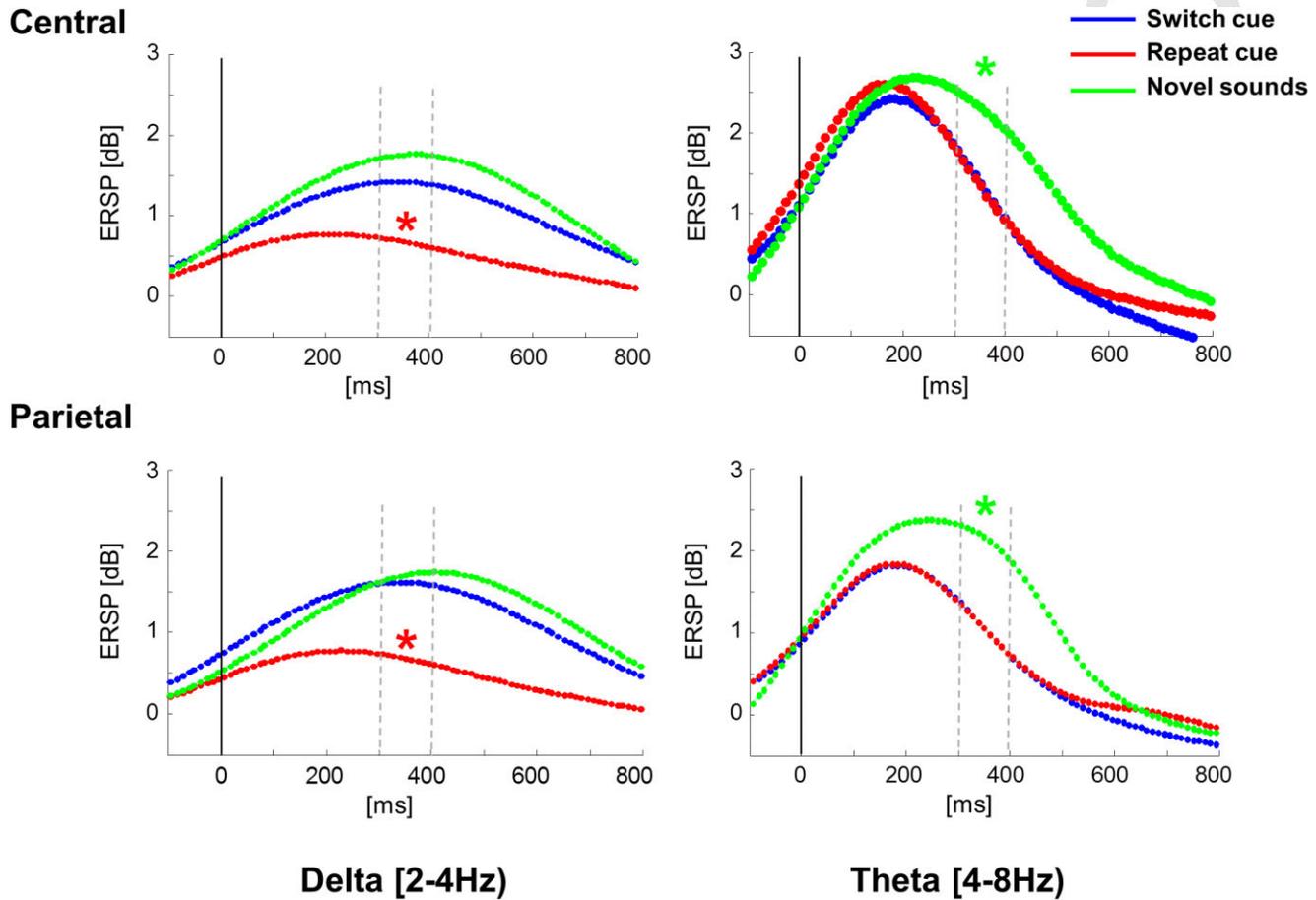


Figure 5. ERSP temporal dynamics for tonal cues and novel sounds. ERSP temporal dynamics calculated for delta and theta frequency ranges at central and parietal regions using the Wavelet_{nc=6} transform. Vertical dotted lines indicate the time window used in the statistical analyses. Asterisks indicate significant differences between conditions ($p < .05$).

and for both wavelet analyses and latency windows, neither significant main effects nor interactions were found ($F_s < 1$).

Figure 8 shows the temporal dynamics of ITC to both cues and novel sounds within the delta and theta frequency ranges at central and parietal regions, starting 200 ms before stimulus onset up to 800 ms poststimulus onset (similar results were found at frontal electrodes). Significant differences between conditions at the nP3 latency window are marked with an asterisk. In sum, phase coherence responses to novel sounds within the nP3 latency window were consistently synchronized to novel stimulus onset across trials, although this was not the case for either tonal switch or repeat cues.

EEG Oscillatory Activity and P300 Amplitude

A linear regression analysis (R^2) was performed to examine the association between the observed changes in ERSP and ITC indexes, and mean nP3 amplitude as the criterion variable for task-cues only (since target P3b amplitudes and ERSP and ITC responses to targets were not sensitive to manipulations of task context). These regression analyses considered data from the central and parietal ROIs, and only from those frequency bands that had previously yielded significant effects (Tables 2 and 3). Mean nP3 amplitudes at central and parietal ROIs were significantly associated with ERSP values only within the delta band

(Figure 9A). For the ITC index within the delta band, only task-switch cues and novel sounds showed a significant correlation with mean nP3 amplitudes at central and parietal ROIs (Figure 9B). For novel sounds, a linear relationship between mean nP3 amplitudes and ITC indexes within the theta and alpha bands was also found. Scatter plots describing these relationships at central ROIs are depicted in Figure 9B. In sharp contrast, mean target P3b amplitudes did not show any significant association with delta ERSP values at central and parietal ROIs either for switch or repeat trials ($R^2_s < .08$, ns).

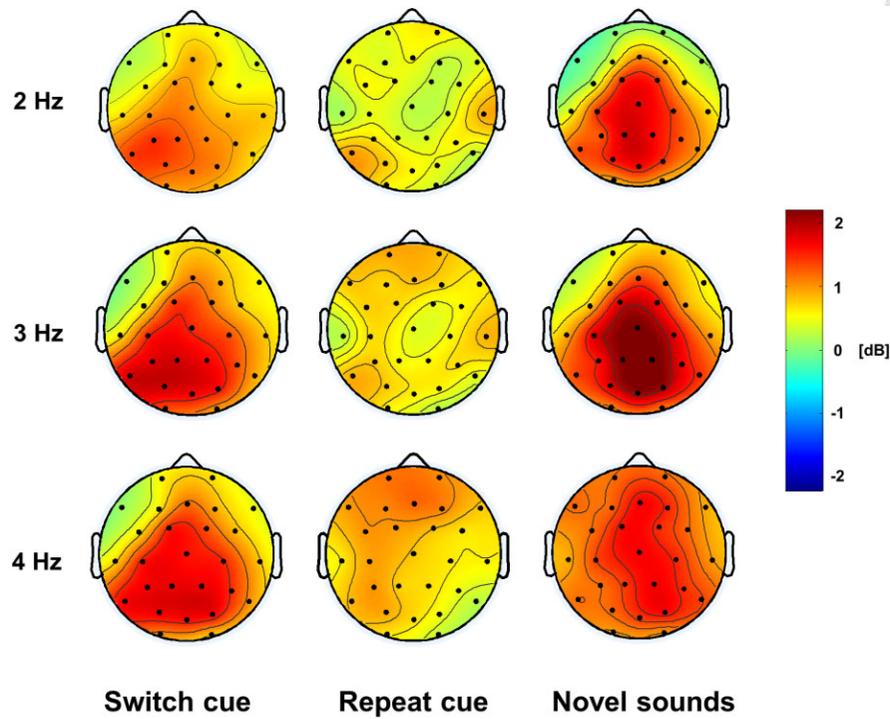
Discussion

We examined the task novelty hypothesis from a time-frequency approach to clarify which of the two aspects of the P300 component traditionally measured in oddball paradigms, either the nP3 or the target P3b, is associated with the conspicuous P300-delta response described in the literature (Basar-Eroglu et al., 1992, 2001; Yordanova et al., 2000). Our main findings can be summarized as follows: (a) strong P300-delta responses were elicited both by infrequent novel sound distracters and by frequent task-switch cues, but not by the equally probable task-repeat cues; (b) target stimuli elicited sizeable target P3b potentials with a typical midparietal scalp distribution, but minimal P300-delta responses;

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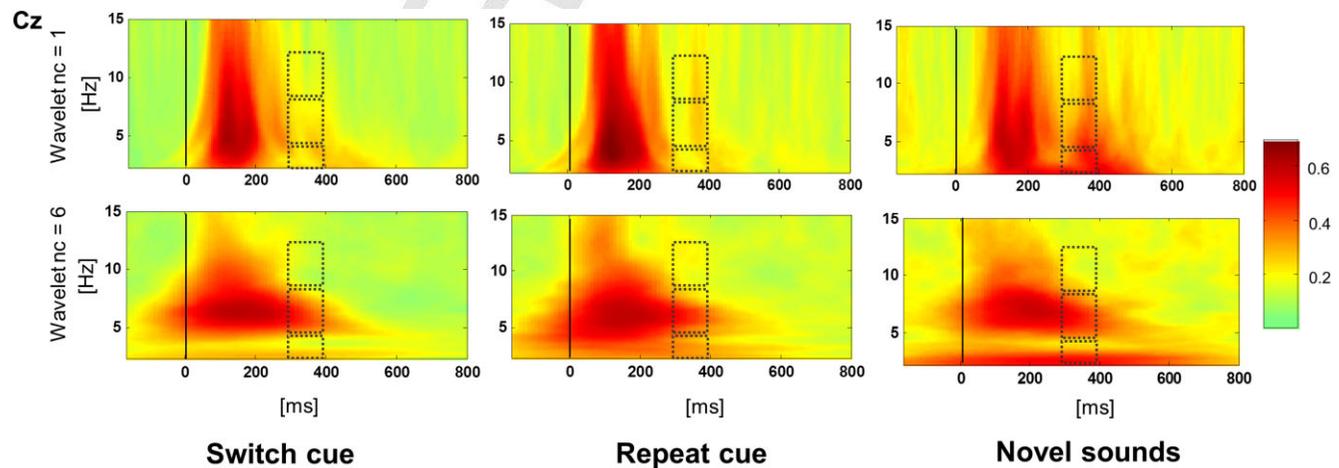


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Figure 6. Scalp maps of signed-RMS power changes across auditory conditions. Signed-RMS power changes across all subjects and scalp channels for switch cues, repeat cues, and novel sounds. Scalp maps show the topography of spectral power changes in decibels within the delta frequency range (2 Hz, 3 Hz, and 4 Hz) for the P300 latency window (330–350 ms poststimulus onset).

(c) crucially, the P300-delta response did not correlate with target P3b amplitude in spite of the substantial intensity of target P3b potentials; (d) the P300-delta response to task-switch cues and novel sounds showed similar frontoparietal distributions, reminiscent of nP3 scalp topography; (e) cue-locked P300-delta responses were sensitive to set-switching manipulations, whereas theta power did not discriminate between task-switch and task-repeat trials; and (f) phase coherence analyses suggested that the P300-delta

response was evoked exogenously by novel sound onset, whereas it was induced endogenously by the onset of task-switch cues. Next, we describe these findings in the context of existing time-frequency analyses of nP3 and target P3b, with special attention to past oddball and task-switching studies. Finally, we put forward the proposal that the P300-delta response may index transient inhibitory control of contextual novelty, and regardless of whether novelty has an endogenous or exogenous origin.



Colour

Figure 7. Intertrial coherence plots for tonal cues and novel sounds. Intertrial coherence plots are shown for task-switch cues, task-repeat cues, and novel sounds at the Cz electrode for EEG frequencies ranging from 2.2–15 Hz. This parameter was analyzed with $\text{Wavelet}_{nc=1}$, offering an optimal temporal resolution, and with $\text{Wavelet}_{nc=6}$, offering an optimal spectral resolution. Auditory stimuli occurred at 0 ms. Greater ITC values are shown in hot colors. The boxes indicate the time and frequency windows used in the statistical analyses.

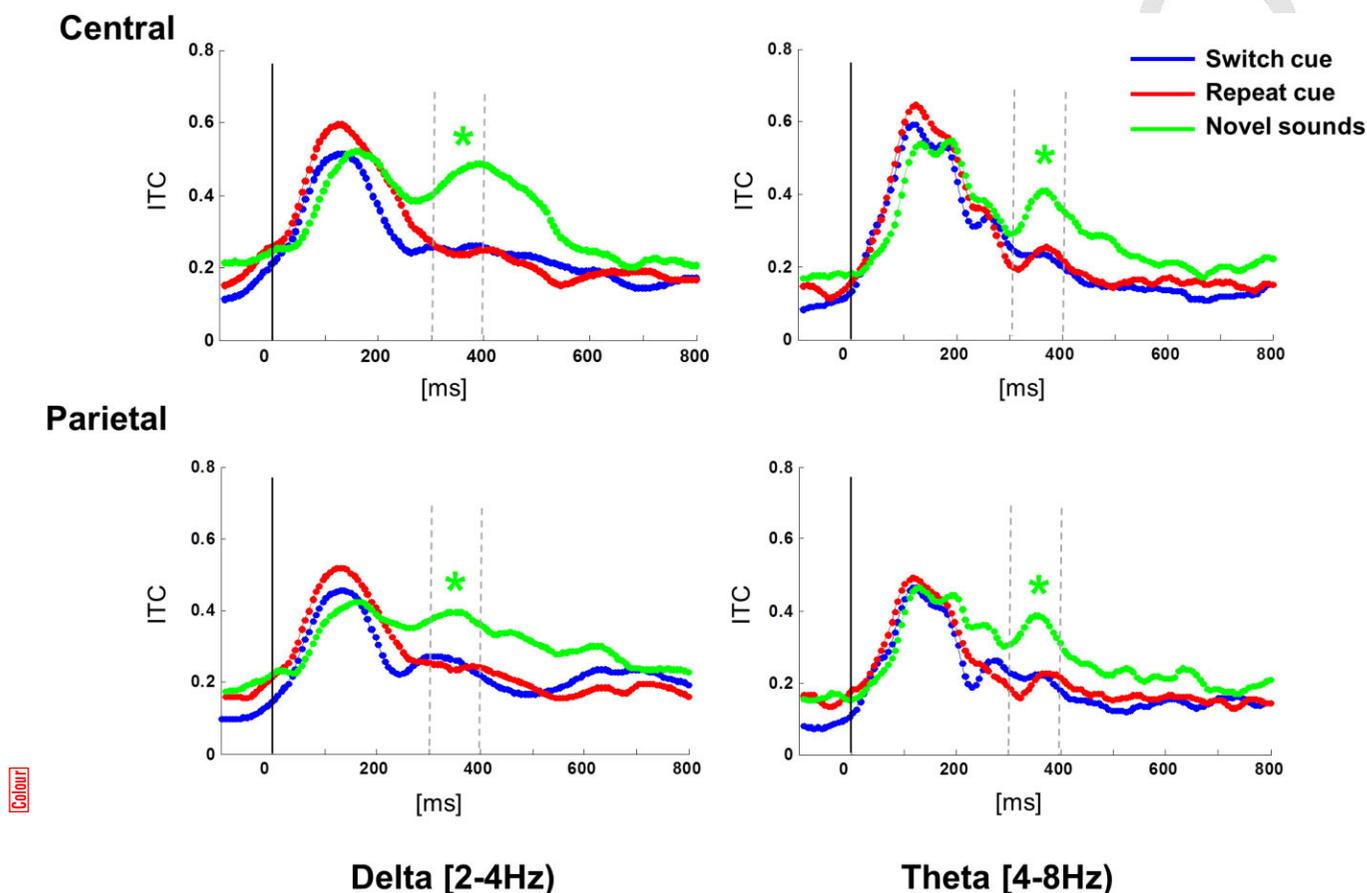


Figure 8. ITC temporal dynamics for tonal cues and novel sounds. ITC temporal dynamics calculated for delta and theta frequency ranges at central and parietal regions using the Wavelet_{inc=1} transform. Vertical dotted lines indicate the time window used in the statistical analyses. Asterisks indicate significant differences between conditions ($p < .05$).

P300-Delta Response Indexes Contextual Novelty

This study adopted a time-frequency approach to pursue further the task novelty hypothesis that the nP3 potential indexes mental set switching in the face of contextual novelty. As in previous ERP studies, mean amplitudes of task-nP3 evoked by the task-switch cues resembled stimulus-nP3 amplitudes evoked by the novel sounds over central and posterior regions (cf. Barcelo et al., 2002, 2006). The analysis of oscillatory neural activity revealed the presence of a strong P300-delta response associated with nP3 potentials to both novel sounds and tonal task-switch cues. These P300-delta responses to switch cues and novel sounds showed similar frontoparietal scalp distributions, reminiscent of the scalp topography of nP3 potentials (Escera et al., 1998, 2000, 2001; Friedman

et al., 2001). On the contrary, neither target stimuli nor task-repeat cues physically identical and with equal overall onset probability as task-switch cues elicited reliable P300-delta responses (Figures 3, 4, 6). Crucially, the P300-delta response did not predict (correlate with) mean target P3b amplitude, in spite of the maximal intensity and midparietal scalp distribution of target P3b potentials. These findings lend support to the task novelty hypothesis that nP3 potentials elicited by both task-switch cues and novel distracters activate a common neural network involved in processing contextual novelty (Barcelo et al., 2002, 2006), since both task-nP3 and stimulus-nP3—but not target P3b—potentials are strongly contributed from delta 2–4 Hz power and/or synchrony (cf. Basar-Eroglu et al., 2001; Yordanova et al., 2000).

Table 2. Linear Regression (R^2) Analyses with ERSF Values as Predictors of Mean nP3 Amplitudes

	Switch		Repeat		Novel	
	Central	Parietal	Central	Parietal	Central	Parietal
Delta	0.46**	0.20	0.32*	0.27*	0.30*	0.46**
Theta	0.003	0.074	0.05	0.004	0.146	0.12

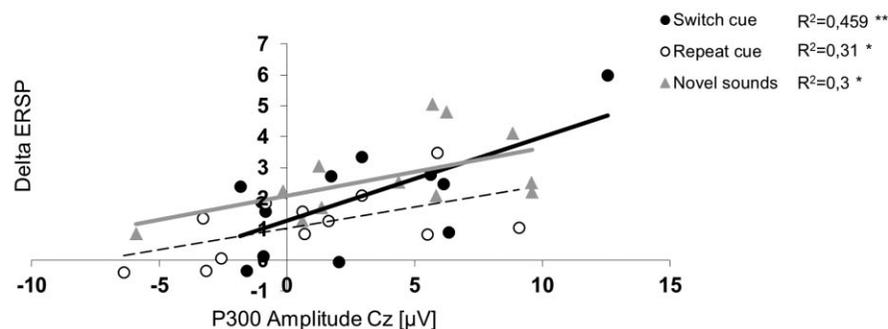
** $p < .01$. * $p < .05$.

Table 3. Linear Regression (R^2) Analyses with ITC Values as Predictors of Mean nP3 Amplitudes

	Switch		Repeat		Novel	
	Central	Parietal	Central	Parietal	Central	Parietal
Delta	0.33*	0.39*	0.014	0.09	0.42*	0.52**
Theta	0.006	0.086	0.035	0.002	0.45**	0.6**
Alpha	0.19	0.015	0.001	0.026	0.27*	0.5**

** $p < .01$. * $p < .05$.

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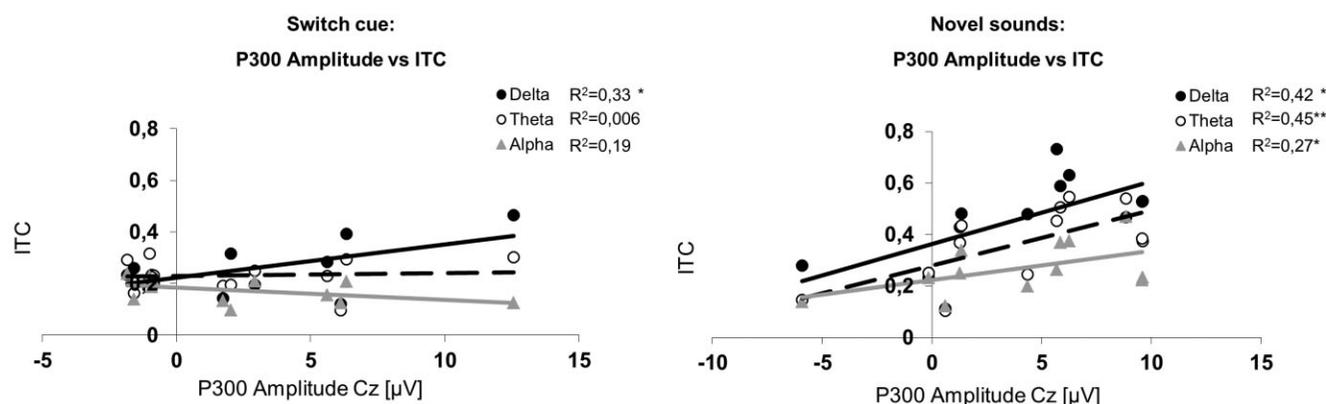


Figure 9. Linear regression (R^2) analyses between nP3 amplitudes and the delta power response at Cz. A: Scatter plot showing the association between mean nP3 amplitude (μV) and delta band ERSP (dB) responses to task-switch cues, task-repeat cues, and novel sounds. ERSP values show a linear increase with increasing nP3 amplitudes, which is strongest after task-switch cues. B: Scatter plot showing the relationship between mean nP3 amplitude (μV) and the ITC index in the delta, theta, and alpha bands in response to task-switch cues and novel sounds. ITC values show a linear increase with increasing nP3 amplitudes for task-switch cues in the delta band, and for novel sounds in the delta, theta, and alpha bands.

Time-frequency EEG analyses have long revealed strong bursts of delta EEG power as one prominent spectral feature of the endogenous P300 potential to infrequent targets delivered on classic two-stimuli oddball paradigms (e.g., Basar-Eroglu et al., 1992; Schürmann et al., 1995; Yordanova & Kolev, 1998a). Those early studies, however, could not decide whether the P300-delta response to oddball targets indexed the processing of rare, surprising, and unexpected stimuli (i.e., event oddballness, novelty P3), as distinct from the processing of motivationally relevant target stimuli (i.e., event targetness, target P3b). These two anatomically and functionally distinct ERP components are typically embedded within the P300 complex and are difficult to extricate without appropriate controls and dedicated signal processing algorithms (Barcelo & Knight, 2007; Makeig et al., 1999). More recent studies compared novel and target events employing variants of the three-stimulus novelty oddball (Demiralp et al., 2001; Isler et al., 2008). For instance, Demiralp et al. (2001) reported modulations of delta and theta power within the nP3 and P3b latency windows in response to both target and novel distracters. These delta (1–4 Hz) power changes showed a frontoparietal scalp distribution with a midparietal maximum and were taken to reflect classic P300 activity. A frontal-central theta (4–8 Hz) component also resembled the scalp topography of the nP3 peak,

mirroring the slow delta response to both novel and oddball targets. More recently, Isler et al. (2008) reported bursts in delta power to both novel and target stimuli relative to standard stimuli delivered in a novelty oddball paradigm, with the largest power differences between novel and standards found within 250-ms poststimulus onset. Interestingly, even though the largest increases in delta power were elicited by novels and targets, these did not elicit differences in delta power in latency windows centered 450 and 670 ms poststimulus onset (see Figure 4, Isler et al., 2008). These similarities suggest that both oddball targets and novels elicit comparable P300-delta responses regardless of their task relevance (Donchin, 1981).

Even though the three-stimulus novelty oddball represents a refinement of the classic oddball task, novel and target stimuli are both infrequent and surprising events, and, hence, early oddball studies could not elucidate whether P300-delta power changes reflect the oddballness or targetness aspects of event processing (Basar-Eroglu et al., 1992; Schürmann et al., 1995; Yordanova & Kolev, 1998a). On the contrary, cued task-switching paradigms are better posed to segregate the distinct and partly overlapping sensory, motor, and sensorimotor processes involved in the preparation and implementation stages of target processing (Barcelo et al., 2006; Barcelo, Perianez, & Nyhus, 2008). In the present

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study, sizeable target-locked P3b amplitudes were measured to both switch and repeat targets, even though these target P3b were not sensitive to the manipulations of task context (i.e., with similar target P3b for switch and repeat trials as shown in Figures 2C, D). Failure to find an association between the P300-delta response and target P3b amplitude concurs with the long-standing functional dissociation between nP3 and target P3b potentials (Barcelo & Knight, 2007; Ranganath & Rainier, 2003). However, our present analyses focused on the upper delta 2–4 Hz range, and, hence, a hypothetical association between lower delta 0.5–2 Hz oscillations and target P3b amplitudes cannot be discarded. Further research is necessary to clarify such a hypothetical dissociation between the contribution of lower and upper delta oscillations towards the generation of target P3b and nP3 potentials, respectively.

Across the delta, theta, and alpha bands, ITC values did not differ significantly between task-switch and task-repeat cues. In contrast, oscillatory brain activity was consistently more synchronized across trials to the onset of novel sounds compared to either switch or repeat cues. Isler et al. (2008) reported a similar effect using an auditory novelty oddball paradigm where novel sounds were randomly intermixed with frequent standard and infrequent target tones. These authors found the largest synchronization for novel sounds, somewhat lesser for targets, and the least synchronization for standard tones. Furthermore, synchronized delta oscillations were phase-coupled to more localized higher frequency oscillations, which was interpreted as a neural mechanism underlying the brain's orienting response (Isler et al., 2008). In line with this interpretation, our time-frequency results suggested a link between the P300-delta response and the neurocognitive mechanisms behind nP3 elicitation. The nP3 component has been traditionally interpreted as an orienting response to unexpected, surprising, or novel distracters (Friedman et al., 2001). On the contrary, Barceló et al. (2002, 2006) reported modulations in nP3 activity to task-switch cues that could be interpreted as a neural correlate of preparatory mental set switching to novel stimulus-response mappings. Likewise, our phase coherence analyses show that the P300-delta response seemed to be induced endogenously by the onset of task-switch cues (Figures 6, 7), whereas it was evoked exogenously by the onset of novel sounds. Indeed, the P300-delta response has been previously shown to reflect self-generated attentional processes (Harmony et al., 1996), and increases in delta power have been observed during endogenous attention towards one's own internal flow of thoughts in short-term memory tasks (Knyazev, 2012). Thus, the existing evidence lends support to the idea that bursts in delta power can be elicited not only exogenously by surprising events in oddball tasks, but also endogenously during preparatory set switching to novel task demands. In all these cases, "contextual novelty" could be conceptualized as "newness" or "recency" of event representations in working memory, and has been mathematically operationalized as Bayesian surprise (cf. Baldi, 2005; Donchin, 1981; Mars et al., 2008). All in all, the present results suggest that P300-delta responses index mental set switching in the face of contextual novelty, and regardless of whether this novelty is conveyed endogenously through new task rules, or exogenously through sensory changes in the environment.

P300-Delta Response Indexes Task Preparation Processes

To our knowledge, this is the first study to apply a time-frequency decomposition to delineate the significance of delta power changes during the preparatory control of task switching. To date, only a

minority of studies have explored brain oscillations to extricate the various and largely overlapping operations involved in task switching (Cunillera et al., 2012; Gladwin & de Jong, 2005; Gladwin et al., 2006; Mansfield et al., 2012; Sauseng et al., 2006), although none of these have examined the role of delta power changes separately during task preparation and implementation stages. In contrast, the vast majority of studies examined the functional role of the P300-delta response using variants of the oddball and go/no-go paradigms (Basar-Eroglu et al., 1992, 2001; Demiralp et al., 1999; Kolev, Demiralp, Yordanova, Ademoglu, & Isoglu-Alkac, 1997; Mathes et al., 2012; Yordanova et al., 2000; Yordanova & Kolev, 1998a). For instance, Yordanova et al. (2000) found an early delta component (labeled "D250") that peaked over central scalp regions, associated with the early P3a component in go/no-go tasks. A longer-latency delta component (labeled "D370") with a midparietal maximum was associated with the auditory target P3b, and was sensitive to task demands. Since novel distracters and task-switch cues can be regarded as no-go signals (cf. Barcelo et al., 2008), our results seem broadly consistent with these early findings, even though we could identify only one single delta blob at maximal spectral resolution (wavelet_{nc=6}; Figure 3). All in all, our time-frequency analyses revealed strong delta power responses to task-switch cues and novel distracters (Figure 3), whereas delta 2–4 Hz power changes faded away in response to the highly predictable visual targets in our cued task-switching paradigm (Figure 4).

Task-cueing paradigms provide a means for isolating brain activations putatively related to two distinct and temporally ordered stages in the top-down control of task-switching, namely, task preparation and task execution processes. In our task-switching paradigm, task cues always predicted target onset at fixed intervals, and, hence, cue-locked EEG power changes offered a measure of event oddballness (i.e., novelty, surprise) relatively uncontaminated from target processes. Likewise, target-locked power changes offer a purer measure of target processes (i.e., target evaluation, response selection, and execution), relatively uncontaminated from event oddballness. This dissociation has shed new light on important aspects on the neurophysiology of cognitive aging (Adrover-Roig & Barcelo, 2010). For instance, Adrover-Roig and Barcelo found that the age-related anterior shift in the scalp distribution of P300 potentials to oddball targets was related to task execution (target P3b) rather than to task preparation (cue-locked nP3) mechanisms. Experimental controls enforced with our cued task-switching paradigm indicate that P300-delta responses were sensitive to manipulations of mental set switching through switch and repeat cues, whereas changes in theta power did not discriminate between these task conditions (Figures 3, 5).

P300-Delta Response Indexes Top-Down Inhibitory Control

The cued task-switching paradigm offers a good means to extricate the neural mechanisms underlying task preparation from task implementation (Barcelo, 2003; Braver, Reynolds, & Donaldson, 2003). The former reflect preparatory or proactive control processes, whereas the latter reflect the exploitation of task-set information available in active working memory networks (Rubinstein et al., 2001). According to the discussion above, the present findings suggest that the P300-delta response does not correlate with the targetness aspects of event processing traditionally associated with the target P3b (i.e., stimulus evaluation, response selection and execution, task engagement). Instead, it is more likely related to the oddballness aspects, and in particular to contextual novelty.

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Moreover, the cued task-switching paradigm is well suited to offer additional information about specific preparatory processes. For instance, since both switch and repeat cues were frequent and equally unexpected events within the trial sequence, neither surprise nor expectancy can be held as major determinants of P300-delta responses. Likewise, motor response inhibition is an unlikely explanation because both switch and repeat cues, as well as novel distracters, all required inhibitory control of overt motor responses (Yordanova et al., 2000). In this regard, Huster et al. (2012) suggested that, given its late onset, the P300-delta response does not qualify for proper motor inhibition, even though nP3 potentials are typically elicited by events that require the inhibition of an overt motor response.

Alternatively, we contend that P300-delta responses may index top-down inhibitory control of old task-set information, such as the previously active S-R mappings at the onset of switch cues, but also the old working memory contents at the onset of a novel distracter. This account is compatible with the purported functional role of delta oscillations in behavioral inhibition (Knyazev, 2012), as both the preparation for a task switch and the appraisal of a novel event likely require the suppression of old working memory contents (Barcelo et al., 2006; Gladwin & de Jong, 2005; Rubinstein et al., 2001; Sauseng et al., 2006). This idea concurs with the purported role of delta oscillations in motor or premotor inhibition in go/no-go and stop trial tasks (Huster et al., 2012; Schmiedt-Fehr & Basar-Eroglu, 2011), as well as in the evaluation of internal and external events with respect to their behavioral saliency and motivational value (Knyazev, 2012). According to this idea, augmented delta activity could index high behavioral relevance of a change in task context or in the saliency of a stimulus (cf. Huster et al., 2012), since both novel distracters and task-switch cues prompt for the suppression of previously active working memory contents, and regardless of whether the new memory contents arise from exogenous or endogenous sources of information.

Contribution from Theta and Alpha Bands to Contextual Novelty

A number of studies have shown a contribution from the theta and alpha bands to elicitation of P300 potentials (Yordanova et al., 2000; Yordanova & Kolev, 1998a, 1998b). For instance, Yordanova et al. (2000) identified two theta sub-bands that correlated with P300 amplitudes, both with a frontal-central scalp distribution. An early theta response (labeled “T250”) was related with early P3a activity as an index of an automatic attentional switch with peak amplitude overlying frontal regions. A late theta response (labeled “T370”) seemed to reflect task-induced activation of working memory contents and was related to the midparietal target P3b. Likewise, our results also revealed distinct increments of early (100–200 ms) and late (300–400 ms) theta power to novel sounds and task cues, with a much reduced late theta response to the target cards (Figures 3, 4). Moreover, our analyses suggested that distracter-locked nP3s were associated with stronger increments in late theta power compared to the task cues. Importantly, neither cue-locked nor target-locked theta power changes differed significantly between switch and repeat trials (Figures 3, 4). Hence, even though theta oscillations may partly contribute to P300 elicitation, they cannot explain the differences in nP3 amplitude between switch and repeat cues. Once again, these discrepancies with earlier results need to be qualified due to the previous confound of the oddballness and targetness

aspects of event processing. All in all, our results are consistent with the purported role of theta phase resetting with neural mechanisms related to the integration of information into working memory (Klimesch, 1999).

Unlike the theta band, we did not find significant differences in alpha power between switch and repeat trials for the time periods explored (i.e., 300–400 ms poststimulus). Moreover, our results are compatible with findings by Gladwin and de Jong (2005) who investigated the development of alpha and theta oscillations during the preparation and execution stages of task switching in the visual and auditory modalities. Their results showed that, when subjects prepared to switch tasks, increases in theta power were accompanied by alpha decreases over occipital regions. Employing an explicit cueing task-switching paradigm, Sauseng et al. (2006) found stronger long-range theta (4–7 Hz) coupling between prefrontal and posterior scalp locations during switch as compared to repeat trials, together with a decrease in upper alpha amplitude (10–13 Hz) during switch trials at posterior scalp regions. These effects were attributed to enhanced processing demands during “access” to long-term memory stores while switching between tasks, as reflected by increased long-range coupling between frontal and posterior brain areas. Our results partly agree with Sauseng et al., as we also found target-locked alpha power decreases in switch compared to repeat trials, although no such effect was apparent during the cue-locked 300–400 ms window explored (Figures 3, 4). However, their study did not segregate brain activity during task preparation and task execution periods, which makes it difficult to derive strong inferences about the functional significance of those effects. Sauseng et al. (2006) also found a pronounced decrease in alpha power (10–13 Hz) during switch trials, which they attributed to larger processing demands during access into long-term memory (also cf. Gladwin & de Jong, 2005, for a similar interpretation). All in all, our theta and alpha power results are consistent with Klimesch’s (1999) proposal that theta synchronization is positively correlated with the ability to encode new information, whereas search and retrieval processes in semantic long-term memory are reflected by upper alpha oscillations in thalamocortical feedback loops (Klimesch, 1999).

Conclusions

The neural responses to task events are not fully captured by ERP, inasmuch as oscillatory neuroelectric signals are not necessarily phase-locked to task events. Thus, a considerable amount of cognitively relevant information in the EEG may be lost in the time-domain averaging, for which reason time-frequency EEG analyses offer important complementary information about neural phenomena (Cohen, 2011; Herrmann et al., 2005; Makeig et al., 2002; Pfurtscheller & Lopes da Silva, 1999). To our knowledge, this is the first study to apply a time-frequency decomposition to examine the significance of delta power changes during the preparatory control of task-switching. More specifically, we examined whether two aspects of the endogenous P300 component traditionally measured in oddball paradigm, namely, the nP3 evoked by contextually novel events and the target P3b to task-relevant target events, are both equally contributed by delta 2–4 Hz oscillations (the so-called P300-delta response). We found strong P300-delta responses elicited both by infrequent novel distracters and by frequent task-switch cues, but not by task-repeat cues nor by target stimuli. Mean target P3b amplitudes showed their typical midparietal distribution but did not differ between switch and

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repeat target trials, nor were they correlated with target-locked changes in delta 2–4 Hz power. These findings suggest that the P300-delta response indexes inhibitory control of mental set

switching in the face of contextual novelty, regardless of whether novelty emerges from endogenous (new task rules) or exogenous (novel distracters) sources of information (cf. Barcelo et al., 2006).

References

- Adrover-Roig, D., & Barcelo, F. (2010). Individual differences in aging and cognitive control modulate the neural indexes of context updating and maintenance during task switching. *Cortex*, *46*, 434–450.
- Baldi, P. (2005). Surprise: A shortcut for attention. In L. Itti, G. Rees, & J. K. Tsotsos (Eds.), *Neurobiology of attention* (pp. 24–28). San Diego, CA: Elsevier Academic Press.
- Barcelo, F. (2003). The Madrid card sorting test (MCST): A task switching paradigm to study executive attention with event-related potentials. *Brain Research. Brain Research Protocols*, *11*, 27–37.
- Barcelo, F., Escera, C., Corral, M. J., & Perianez, J. A. (2006). Task switching and novelty processing activate a common neural network for cognitive control. *Journal of Cognitive Neuroscience*, *18*, 1734–1748.
- Barcelo, F., & Knight, R. T. (2007). An information-theoretical approach to contextual processing in the human brain: Evidence from prefrontal lesions [Supplement 1]. *Cerebral Cortex*, *17*, i51–i60.
- Barcelo, F., Perianez, J. A., & Knight, R. T. (2002). Think differently: A brain orienting response to task novelty. *NeuroReport*, *13*, 1887–1892.
- Barcelo, F., Perianez, J. A., & Nyhus, E. (2008). An information theoretical approach to task-switching: Evidence from cognitive brain potentials in humans. *Frontiers in Human Neuroscience*, *1*, 13.
- Basar-Eroglu, C., Basar, E., Demiralp, T., & Schürmann, M. (1992). P300-response: Possible psychophysiological correlates in delta and theta frequency channels: A review. *International Journal of Psychophysiology*, *13*, 161–179.
- Basar-Eroglu, C., Demiralp, T., Schürmann, M., & Basar, E. (2001). Topological distribution of oddball ‘P300’ responses. *International Journal of Psychophysiology*, *39*, 213–220.
- Braver, T. S., Reynolds, J. R., & Donaldson, D. I. (2003). Neural mechanisms of transient and sustained cognitive control during task switching. *Neuron*, *39*, 713–726.
- Cohen, M. X. (2011). It’s about time. *Frontiers in Human Neuroscience*, *5*, 2.
- Cunillera, T., Fuentemilla, L., Perianez, J., Marco-Pallares, J., Kramer, U. M., Camara, E., . . . Rodriguez-Fornells, A. (2012). Brain oscillatory activity associated with task switching and feedback processing. *Cognitive, Affective, and Behavioral Neuroscience*, *12*, 16–33.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21.
- Demiralp, T., Ademoglu, A., Isteфанopoulos, Y., Basar-Eroglu, C., & Basar, E. (2001). Wavelet analysis of oddball P300. *International Journal of Psychophysiology*, *39*, 221–227.
- Demiralp, T., Ademoglu, A., Schürmann, M., Basar-Eroglu, C., & Basar, E. (1999). Detection of P300 waves in single trials by the wavelet transform (WT). *Brain and Language*, *66*, 108–128.
- Donchin, E. (1981). Surprise! . . . Surprise? *Psychophysiology*, *18*, 493–513.
- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology & Neuro-Otology*, *5*, 151–166.
- Escera, C., Alho, K., Winkler, I., & Naatanen, R. (1998). Neural mechanisms of involuntary attention to acoustic novelty and change. *Journal of Cognitive Neuroscience*, *10*, 590–604.
- Escera, C., Yago, E., & Alho, K. (2001). Electrical responses reveal the temporal dynamics of brain events during involuntary attention switching. *European Journal of Neuroscience*, *14*, 877–883.
- Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain’s evaluation of novelty. *Neuroscience and Biobehavioral Reviews*, *25*, 355–373.
- Gladwin, T. E., & de Jong, R. (2005). Bursts of occipital theta and alpha amplitude preceding alternation and repetition trials in a task-switching experiment. *Biological Psychology*, *68*, 309–329.
- Gladwin, T. E., Lindsen, J. P., & de Jong, R. (2006). Pre-stimulus EEG effects related to response speed, task switching and upcoming response hand. *Biological Psychology*, *72*, 15–34.
- Harmony, T., Fernandez, T., Silva, J., Bernal, J., Diaz-Comas, L., Reyes, A., . . . Rodriguez, M. (1996). EEG delta activity: An indicator of attention to internal processing during performance of mental tasks. *International Journal of Psychophysiology*, *24*, 161–171.
- Herrmann, C. S., Busch, N. A., & Grigutsch, M. (2005). EEG oscillations and wavelet analysis. In T. C. Handy (Ed.), *Event-related potentials: A methods handbook* (pp. 229–259). Cambridge, MA: MIT Press.
- Huster, R. J., Enriquez-Geppert, S., Lavalley, C. F., Falkenstein, M., & Herrmann, C. S. (2012). Electroencephalography of response inhibition tasks: Functional networks and cognitive contributions. *International Journal of Psychophysiology*, *87*, 217–233.
- Isler, J. R., Grieve, P. G., Czernochowski, D., Stark, R. I., & Friedman, D. (2008). Cross-frequency phase coupling of brain rhythms during the orienting response. *Brain Research*, *1232*, 163–172.
- Jennings, J. R. (1987). Editorial policy on analyses of variance with repeated measures. *Psychophysiology*, *24*, 474–475.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29*, 169–195.
- Knyazev, G. G. (2012). EEG delta oscillations as a correlate of basic homeostatic and motivational processes. *Neuroscience and Biobehavioral Reviews*, *36*, 677–695.
- Kolev, V., Demiralp, T., Yordanova, J., Ademoglu, A., & Isoglu-Alkac, U. (1997). Time-frequency analysis reveals multiple functional components during oddball P300. *NeuroReport*, *8*, 2061–2065.
- Makeig, S., Westerfield, M., Jung, T.-P., Covington, J., Townsend, J., Sejnowski, T. J., & Courchesne, E. (1999). Functionally independent components of the late positive event-related potential during visual spatial attention. *Journal of Neuroscience*, *19*, 2665–2680.
- Makeig, S., Westerfield, M., Jung, T. P., Enghoff, S., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2002). Dynamic brain sources of visual evoked responses. *Science*, *295*, 690–694.
- Mansfield, E. L., Karayanidis, F., & Cohen, M. X. (2012). Switch-related and general preparation processes in task-switching: Evidence from multivariate pattern classification of EEG data. *Journal of Neuroscience*, *32*, 18253–18258.
- Mars, R. B., Debener, S., Gladwin, T. E., Harrison, L. E., Haggard, P., Rothwell, J. C., & Bestmann, S. (2008). Trial-by-trial fluctuations in the event-related encephalogram reflect dynamic changes in the degree of surprise. *Journal of Neuroscience*, *28*, 12539–12545.
- Mathes, B., Schmiadt, J., Schmiadt-Fehr, C., Pantelis, C., & Basar-Eroglu, C. (2012). New rather than old? For working memory tasks with abstract patterns the P3 and the single-trial delta response are larger for modified than identical probe stimuli. *Psychophysiology*, *49*, 920–932.
- Perianez, J. A., & Barcelo, F. (2009). Updating sensory versus task representations during task-switching: Insights from cognitive brain potentials in humans. *Neuropsychologia*, *47*, 1160–1172.
- Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*, 1842–1857.
- Ranganath, C., & Rainier, G. (2003). Neural mechanisms for detecting and remembering novel events. *Nature Reviews in Neuroscience*, *4*, 193–202.
- Rubinstein, J. S., Meyer, D. E., & Evans, J. E. (2001). Executive control of cognitive processes in task switching. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 763–797.
- Sauseng, P., Klimesch, W., Freunberger, R., Pecherstorfer, T., Hanslmayr, S., & Doppelmayr, M. (2006). Relevance of EEG alpha and theta oscillations during task switching. *Experimental Brain Research*, *170*, 295–301.
- Schmiadt-Fehr, C., & Basar-Eroglu, C. (2011). Event-related delta and theta brain oscillations reflect age-related changes in both a general and a specific neuronal inhibitory mechanism. *Clinical Neurophysiology*, *122*, 1156–1167.
- Schürmann, M., Basar-Eroglu, C., Kolev, V., & Basar, E. (1995). A new metric for analyzing single-trial event-related potentials (ERPs): Application to human visual P300 delta response. *Neuroscience Letters*, *197*, 167–170.

P300-delta response indexes contextual novelty

15

1 Schürmann, M., Basar-Eroglu, C., Kolev, V., & Basar, E. (2001). Delta
2 responses and cognitive processing: Single-trial evaluations of human
3 visual P300. *International Journal of Psychophysiology*, 39, 229–239.
4 Verstraeten, E., & Cluydts, R. (2002). Attentional switching-related human
5 EEG alpha oscillations. *NeuroReport*, 13, 681–684.
6 Yordanova, J., Devrim, M., Kolev, V., Ademoglu, A., & Demiralp, T.
7 (2000). Multiple time-frequency components account for the complex
8 functional reactivity of P300. *NeuroReport*, 11, 1097–1103.

Yordanova, J., & Kolev, V. (1998a). Event-related alpha oscillations are
functionally associated with P300 during information processing.
NeuroReport, 9, 3159–3164.
Yordanova, J., & Kolev, V. (1998b). Single-sweep analysis of the theta
frequency band during an auditory oddball task. *Psychophysiology*, 35,
116–126.

(RECEIVED October 6, 2013; ACCEPTED February 11, 2014)

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