

Theta lingua franca: A common mid-frontal substrate for action monitoring processes

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Abstract

We present evidence that a multitude of mid-frontal event-related potential (ERP) components partially reflect a common theta band oscillatory process. Specifically, mid-frontal ERP components in the N2 time range and error-related negativity time range are parsimoniously characterized as reflections of theta band activities. Forty participants completed three different tasks with varying stimulus–response demands. Permutation tests were used to identify the dominant time–frequency responses of stimulus- and response-locked conditions as well as the enhanced responses to novelty, conflict, punishment, and error. A dominant theta band feature was found in all conditions, and both ERP component amplitudes and theta power measures were similarly modulated by novelty, conflict, punishment, and error. The findings support the hypothesis that generic and reactive medial prefrontal cortex processes are parsimoniously reflected by theta band activities.

Descriptors: ERN, FRN, N2, Theta, Anterior cingulate, Conflict, Reinforcement learning

A convergence of evidence from multiple levels of the neural sciences has identified a system for action monitoring in medial prefrontal cortex (mPFC), particularly anterior cingulate cortex (ACC). This system has been described as a functional node in complex processes such as adaptive control over behavior and acquisition of reinforcement contingencies, as a dynamic processing hub for attention and action selection, and as a sensitive determinant of motivational functions, including emotional reactivity and willful engagement. This function of the ACC may succinctly be described by the integration of contextual cues with action selection to optimize goal-driven performance (Carter et al., 1998; Devinsky, Morrell, & Vogt, 1995; Paus, 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Rushworth, Buckley, Behrens, Walton, & Bannerman, 2007).¹ An extensive literature of

human studies has detailed a series of event-related potential (ERP) components that putatively reflect mPFC/ACC operations during attention, cognitive control, feedback learning, and action selection. Here, we specifically focus on ERP components relevant to formal models of reinforcement learning (Holroyd & Coles, 2002) and conflict monitoring (Yeung, Botvinick, & Cohen, 2004). These ERP features are reviewed below, and it is suggested that these components might all be reflections of general mPFC processes as indicated by frontal theta.

Stimulus-Locked Components

The only stimulus-locked components detailed here are ones that occur over mid-frontal regions in the N2 time range (negative deflections peaking ~250–350 ms poststimulus). To characterize the variety of “N2-like” frontal voltage potentials occurring in this time range, the distinction made by Folstein and Van Petten (2008) will be used. Folstein and Van Petten described two broad classes of anterior N2s: one class involved in action selection (control N2) and another relating to attention (mismatch N2). The control-related N2 component is modulated by stimuli indicating variations in stimulus–response demand: for example, a stimulus that primes multiple competing motor responses (Yeung, Botvinick, et al., 2004). The mismatch-related N2 component is modulated by stimuli that reflect an unexpected perceptual differentiation: for example, a novel stimulus occurring in a train of standards on an

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1. Although Vogt (2005) has developed a new nomenclature to parse the cingulate cortex into regions and subregions based on functional distinction, this investigation does not aim to interpret the spatial specificity of EEG signals or reinterpret the findings from previously published works. As such, we use the broad term “mPFC” when inferring the source contribution of EEG data recorded at the FCz electrode, and we use the anatomical

terminology specific to each citation when detailing prior findings. Note that many subsequent descriptions of ACC activation may actually occur in Vogt’s “mid cingulate” area, not the peri- and subgenual “anterior cingulate” area.

oddball task. Another action monitoring component that shares features with both the control and mismatch N2 is the feedback-related negativity (FRN), a fronto-central negativity occurring after feedback that indicates poor performance or a loss of value (Holroyd & Coles, 2002). Parallels between the FRN and the mismatch N2 have been frequently noted in the literature, particularly due to the similar eliciting factors and spatiotemporal patterns of these components. Holroyd, Pakzad-Vaezi, and Krigolson (2008) have recently suggested that the FRN is simply an N2 that occurs to unexpected negative feedback. As with the N2, infrequency and degree of mismatch modulate the FRN; however, it is unknown if these eliciting events reflect alterations of different underlying neural processes (Donkers, Nieuwenhuis, & van Boxtel, 2005; Donkers & van Boxtel, 2004; Holroyd, 2004). In fact, all of these fronto-central negativities appear to be sensitive to a form of expectation mismatch, although they may differ in terms of attention orientation (mismatch N2), action selection (control N2), or punishment prediction error (FRN). Although these mismatch signals may reflect disparate processes in unique cognitive circumstances, these aforementioned processes have all been specifically associated with ACC function during attention orientation and/or action selection (Carter et al., 1998; Devinsky et al., 1995; Paus, 2001; Ridderinkhof et al., 2004; Rushworth et al., 2007).

Response-Locked Components

In motivated performance tasks, an error of motor commission elicits an error-related negativity (ERN), a negative voltage deflection peaking around 80 ms postresponse (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993). A smaller negativity has been found on correct trials, sometimes termed the correct related negativity (CRN). CRNs have been proposed to reflect an inherent feature of the ACC response to manual responses in a demanding task (Cavanagh, Cohen, & Allen, 2009; Vidal, Burle, Bonnet, Grapperon, & Hasbroucq, 2003; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000; Yordanova, Falkenstein, Hohnsbein, & Kolev, 2004). Both the ERN and CRN are larger under conditions of increased task difficulty (Hajcak, Moser, Yeung, & Simons, 2005), but the formal differentiation between the two becomes nondistinct in ambiguous cases. The amplitude of the ERN and the CRN are reciprocally related to uncertainty (Pailing & Segalowitz, 2004), and suboptimal choices on reinforcement learning tasks yield a larger voltage potential than correct responses as the task become learned, although this suboptimal “error” is much smaller than a motor error-of-commission (Frank, Woroch, & Curran, 2005; Gründler, Cavanagh, Figueroa, Frank, & Allen, 2009; Holroyd & Coles, 2002). Experimental context appears to dynamically modulate these features of response-locked ERPs along a continuum, suggesting that all of these response-related components appear to reflect a similar underlying process that is particularly sensitive to conflict or error.

Plethora of Potentials or Possible Parsimony?

To date, there is no inclusive theory or model on the collection of mid-frontal negativities commonly described as the ERN, CRN, FRN, and N2. Although the terminological distinctions of “ERN,” “N2,” and so forth have proven useful in defining specific spatiotemporal ERP components, interpretations of the functional processes reflected by these signals may be hindered by the abundant terminology of seemingly different task-specific components. For

example, a small set of cognitive functions may be shared between the reinforcement learning (Holroyd & Coles, 2002) and conflict monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Yeung, Botvinick, et al., 2004) processes, although these commonalities may be obscured by methods of quantification and choice of theoretical reference frame. A parsimonious summary could propose that both the stimulus- and response-related fronto-central negativities reflect common features of the processing demands of the mPFC, especially the ACC. These features are varied across systems related to cognitive and motor control, attention, and reinforcement learning, but are especially sensitive to mismatch signals of conflict, punishment, and error in the service of behavioral adaptation. Fitting with this account, a single mid-frontal EEG signal has been shown to be sensitive to these conditions and has been suggested to be reflected within all of these aforementioned ERP components: frontal theta.

A Common Theta Substrate?

Talairach et al. (1973) described how electrical stimulation of the human ACC elicited motor actions that were integrated with environmental context, sometimes accompanied by mid-frontal theta oscillatory activities recorded in the EEG. A growing literature has identified the frontal midline theta rhythm in the generation of event related mid-frontal voltage negativities during conflict and error responses. The ACC has been shown to generate neural oscillations in the theta band (Tsujimoto, Shimazu, & Isomura, 2006; Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005; Womelsdorf et al., 2007), and these oscillations have been linked to multiple processes, including memory, attention, learning, and action selection (Cohen, Ridderinkhof, Haupt, Elger, & Fell, 2008; Debener et al., 2005; Marco-Pallares et al., 2008; Onton, Delorme, & Makeig, 2005; Wang et al., 2005). The ERN has been proposed to reflect a degree of theta phase consistency and power enhancement over the medial frontal cortex (Cavanagh et al., 2009; Luu & Tucker, 2001; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Luu, Tucker, & Makeig, 2004; Trujillo & Allen, 2007; Yordanova et al., 2004), as have the CRN (Burle, Roger, Allain, Vidal, & Hasbroucq, 2008; Cavanagh et al., 2009; Yordanova et al., 2004), the FRN (Bernat, Nelson, Holroyd, Gehring, & Patrick, 2008; Cavanagh, Frank, Klein, & Allen, 2010; Cohen, Elger, & Ranganath, 2007; Marco-Pallares et al., 2008), and the N2 (Cavanagh et al., in press; Cohen et al., 2008). These commonalities suggest that the distinct components defined as the ERN, CRN, FRN, and N2 may reflect variants of a similar underlying neural process, namely, mid-frontal theta.

Any ERP can reflect a unique combination of power enhancement and phase consistency of underlying processes (Fell et al., 2004; Le Van Quyen & Bragin, 2007; Makeig, Debener, Onton, & Delorme, 2004; Sauseng et al., 2007). Advanced signal processing techniques (such as wavelet convolution, short-time Fourier transform, or the Hilbert transform) can parse frequency-specific power and phase relationships within the EEG signal. Although these time-frequency methods cannot alone determine if a signal is oscillatory in nature (Ritter & Becker, 2009; Sauseng et al., 2007; Yeung, Bogacz, Holroyd, & Cohen, 2004; Yeung, Bogacz, Holroyd, Nieuwenhuis, & Cohen, 2007), they can disambiguate band-specific signals recorded at any single electrode. These methodological steps reveal dimensions of the EEG signal (frequency, power, and phase) that are proposed to reflect separable physiological mechanisms for the organization and communication of neural computations (Buzsáki, 2006; Buzsáki & Draguhn, 2004; Fries,

2005; Womelsdorf et al., 2007). In this article it will be argued that there are theoretical and practical benefits for using such a time-frequency approach to interpret the functional roles of these action-monitoring ERP components. We introduce the hypothesis that mid-frontal theta phase dynamics reflect common templates for the temporal organization of neural responses to stimuli and responses, with variations on this template reflecting neural reactions to novelty, conflict, punishment, and error.

The Current Study

Here we aimed to formally compare a wide variety of mid-frontal responses to stimuli and actions with multiple measures of event-related EEG. Given the broad role of the mPFC in merging cognitive and motor functions, it was hypothesized that a multitude of different action-monitoring events would elicit mid-frontal EEG responses. However, like the mPFC, it was proposed that these EEG responses would be particularly sensitive to signals of novelty, conflict, punishment, and error. Data-driven permutation tests were used to provide statistical evidence of dominant time-frequency responses associated with specific ERP components. Permutation tests were also used to identify the enhanced EEG responses to conditions of novelty, conflict, punishment, and error. A dominant theta band feature was found in all experimental conditions, and both ERP component amplitudes and theta power measures were similarly modulated by novelty, conflict, punishment, and error. The findings supported the hypothesis that generic and reactive mPFC processes are parsimoniously reflected by theta band activities.

Methods

Participants

Participants were 40 students (12 female) with a mean age of 19.18 years ($SD = 1.13$) who participated for course credit. All participants gave informed consent, and the research ethics committee of the University of Arizona approved the study. All participants were free of past head trauma or seizures and free of current psychoactive medication use.

Procedures

First, participants filled out questionnaires and supplied demographic information. Second, the EEG cap was applied and participants sat quietly for 6 min while resting EEG was recorded. Finally, participants completed three different sets of tasks (each described below) in a randomized counterbalanced order. The entire study lasted 2 h, with each active task taking approximately 20 min with short self-paced breaks between tasks.

Perception and Motor Tasks

There were two mixed tasks in this set (Figure 1a). For the three oddball task blocks, participants were instructed to place their response buttons in their laps; no responses were required. Blocks consisted of 15, 20, or 25 targets (red Os) occurring at ~14% probability (60 total) that participants were instructed to count. Standards (blue Xs) were presented on ~72% of trials (311 total); surprise novel stimuli (varied colored shapes) were presented on ~14% of trials (60 total). All stimuli were presented for 500 ms with a jittered intertrial interval (ITI) of 500–1300 ms. The response task consisted of two blocks intermixed between oddball

blocks. Each block instructed participants to pick up either the left or right button and simply press it every second or two. For EEG analysis, data were locked to the cues in the oddball task and the responses in the response tasks. These tasks provide measures of stimulus processing independent of motor responding (oddball task) and single motor responses independent of stimulus processing.

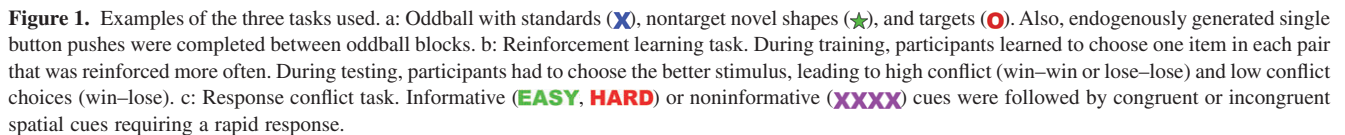
Probabilistic Learning Task

The probabilistic learning task consisted of brief forced-choice training blocks consisting of 16 trials, each followed by a subsequent testing block with 16 trials (modified from Frank, Seeberger, & O'Reilly, 2004; see Figure 1b). There were eight of these train/test blocks. During each training block the participants were presented with two pictures (hereafter cues), where each cue was associated with a different probabilistic chance of receiving "Correct" or "Incorrect" feedback. These cue pairs (and their probabilities of reward) were termed A/B (87.5%/12.5%) and C/D (62.5%/37.5%). All training trials began with a jittered ITI between 1000 and 1500 ms. Each cue pair then appeared for a maximum of 4000 ms and disappeared immediately after the choice was made. Following a button press, either "Correct" or "Incorrect" feedback was presented for 1000 ms (jittered between 100 and 200 ms after response). If the participant failed to make a choice within the 4000 ms, "No Response Detected" was presented. Over the course of the training block, participants typically learned to choose A over B and C over D based on adaptive responding to feedback.

During the testing blocks all possible novel combinations of cue pairs from the previous training block (e.g., AD, CB, etc.) were presented four times each (16 trials total), and no feedback was provided. All training trials began with a jittered ITI between 1000 and 1500 ms. Each cue pair then appeared for a maximum of 4000 ms, and disappeared immediately after the choice was made. These cue pairs were sorted into separate conditions based on reinforcement conflict: high conflict (consisting of both win-win trials [AC] and lose-lose trials [BD]) and low conflict (consisting of win-lose trials [AB or CD]). For EEG analyses, cue- and response-locked data were taken from the test phase, but feedback-locked data were taken from the training phase. Cue- and response-locked trials were only included if the response times (RTs) were between 200 ms and 4000 ms. Response-locked high- and low-conflict trials consisted of correctly identified (optimal) choices, whereas the suboptimal trials condition consisted of all trials that were incorrectly identified.

Response Competition Task

A modified Simon task (Simon & Rudell, 1967) with preparatory cues was used to assess response competition processes (Figure 1c). Each trial began with an equiprobable informative cue (green "EASY," red "HARD," or purple "XXXX"), indicating that the trial would require a congruent or incongruent response or, in the case of purple Xs, that the response was equiprobably congruent or incongruent. Informative cues were presented for 2000 ms, after which the imperative cue was presented to the left or right side of the screen (yellow circle for left response, blue square for right response) for 250 ms, whereupon a blank screen was presented for 250 ms. Participants had this total 500-ms window in which to respond. All trials had an ITI of 1000 ms, but erroneous responses had an additional delay of 1000 ms followed by "Incorrect" feedback presented for 1000 ms, and nonresponses had "Faster!" feed-



Time–frequency calculations were computed using custom-written Matlab routines (Cavanagh et al., 2009; Cohen et al., 2008). Time–frequency measures were computed by multiplying the fast Fourier transformed (FFT) power spectrum of single-trial EEG data with the FFT power spectrum of a set of complex Morlet wavelets (defined as a Gaussian-windowed complex sine wave: $e^{-i2\pi f t} e^{-t^2/(2\sigma^2)}$, where t is time, f is frequency (which increased

2. All results were similar when compared to current source density-transformed EEG.

from 1 to 50 Hz in 50 logarithmically spaced steps), and σ defines the width (or “cycles”) of each frequency band, set according to $4/(2\pi f)$, and taking the inverse FFT. The end result of this process is identical to time-domain signal convolution, and it resulted in (a) estimates of instantaneous power (the magnitude of the analytic signal), defined as $Z[t]$ (power time series: $p(t) = \text{real}[z(t)]^2 + \text{imag}[z(t)]^2$) and (b) phase (the phase angle) defined as $\phi_i = \arctan(\text{imag}[z(t)]/\text{real}[z(t)])$. The time and frequency resolutions of different center frequencies can be calculated as $2\sigma_t$ and $2\sigma_f$ (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997; Yordanova et al., 2004). In the theta range, these resolutions ranged from 322 ms and 2 Hz (centered at 4 Hz) to 157 ms and 4 Hz (centered at 8 Hz).

Each epoch was then cut in length (−500 to +1000 ms). Power was normalized by conversion to a decibel (dB) scale ($10 * \log_{10}[\text{power}(t)/\text{power}(\text{baseline})]$), allowing a direct comparison of effects across frequency bands. The baseline for each frequency consisted of the average power from −500 to −400 ms prior to the onset of the cues (responses for each task were baseline-corrected to task-specific precue baselines; in the single response condition these were baseline corrected to the precue oddball baseline). Whereas the ERPs reflect phase-locked amplitude changes, these time–frequency measures reflect total power (phase-locked and phase-varying).

Intertrial phase coherence was used to measure the consistency of phase values for a given frequency band at each point in time (Lachaux, Rodriguez, Martinerie, & Varela, 1999). Intertrial phase coherence values vary from 0 to 1, where 0 indicates random phases at that time–frequency point across trials, and 1 indicates identical phase values at that time–frequency point across trials. Intertrial phase coherence (also termed the phase-locking value [PLV]) at each time point is defined as

$$PLV = \left| \frac{1}{n} * \sum_{x=1}^n e^{i\phi_x} \right|,$$

where n is the number of trials for each time and each frequency band. PLV thus reflects the extent to which oscillation phase values are consistent over trials at that point in time–frequency space (power, in contrast, represents the intensity of that signal). This investigation additionally used the Hilbert transform to compute the PLV over time between *conditions* for filtered ERPs to assess the degree of band-specific phase-locking in ERPs (see Figure 5c, below).

Statistical Analysis

First, permutation tests were performed on the voltage difference over time and frequency between rest and task-specific conditions using custom-written Matlab routines. This process tested the null hypothesis that the data in the rest and task conditions are interchangeable. Results therefore indicate how task-related activity differs from intrinsic (task-unrelated) EEG processes. First, paired-sample t tests were computed at each time–frequency point (pixel) between the grand average empirical task data and rest. This procedure matched the epoch counts between comparisons (by randomly selecting from the pool of the larger set) in order to control for unequal weightings of evidence. Because the resting data had a mean and median of 120 epochs, it was the larger set in all cases except for oddball standards. Only pixels that survived $p < .05$ thresholding were retained. Multiple comparison correction of the empirical tests were completed using permutation tests of weighted

cluster-based thresholding, sometimes known as the “exceedance mass” (Nichols & Holmes, 2002). One thousand permutations were run for each condition. Within each permutation, t tests were computed between data sets that had been randomly shuffled between rest and task conditions. Each permutation also used conditions with the same number of epochs. The sum of the t values within each cluster of significant pixels (the “mass”) was used to threshold the empirical data. The top 2.5% of mass values for each of the 1000 permutations were used as the threshold, separately for positive and negative clusters, providing a two-tailed 5% alpha level of family-wise error control for multiple comparison correction. This method provides a data-driven hypothesis test that identifies where conditions differ from rest over time–frequency space. Figures 3 and 4, below, show these comparisons for each task and condition (vs. rest).

Next, key comparisons were made between relevant conditions to identify if novelty, conflict, punishment, and error conditions demonstrate different EEG activities than respective comparison conditions. Epoch counts were matched between conditions as described above. In all of these planned comparisons, stimulus-locked high- and low-conflict trials on the response conflict task were taken following noninformative (XXXX) cues to control for differential expectations that would be present on EASY or HARD trials. Differences between conditions were assessed by the permutation testing methods described above, but this time shuffling between relevant conditions (e.g., shuffling between error and correct trials; see Figures 5 and 6, below).

Three different methods were used to compare the performance of ERP and theta power measurements. First, a factor analysis was used to examine the degree of *between-measurement* variation *within tasks* in order to determine if ERP and theta measurements loaded on similar factors. Two different factor analyses of ERP amplitudes and theta power were performed: one on all 19 variables of interest and a second on 10 difference scores. Varimax rotation was used to derive orthogonal factors in order to highlight within-task effects. Variables were included in each factor if they had a loading greater than an absolute value of .3. Because this factor analysis includes a large number of variables with a modest number of participants, these tests should be interpreted with caution. Second, both ERP amplitudes and region-of-interest (ROI) defined theta power were used to assess differences between conditions (Figure 8, below). In this ROI analysis, theta power was taken from similarly sized windows on the grand-average time plots between the time ranges that were used for ERP component selection (Figures 3 and 4, below; 4–8 Hz, stimulus-locked: 200 to 350 ms, response-locked: −24 to 124 ms). Third, power analyses were computed on the theta power and ERP effect sizes for novelty, conflict, punishment, and error conditions (Figure 9, below).

Results

Performance

On average, participants were 100% correct in their count of oddball targets ($SD = 2\%$). All participants were >55% accurate in the low-conflict test phase condition on the reinforcement learning task. On the reinforcement learning task, high-conflict trials (win–win and lose–lose) had significantly slower RTs than low-conflict (win–lose) trials, $t(39) = 2$, $p < .05$, and they were also characterized by poorer accuracy, $t(39) = -8.94$, $p < .001$. Whereas the accuracy difference from low-conflict trials was similarly large for

win–win and lose–lose valences (both $t_s > -7.5$, $p_s < .001$), RT was only slower on lose–lose trials, $t(39) = 3.6$, $p < .001$, not win–win trials, $t(39) < 1$. A highly similar pattern of effects on this same task has been found in Parkinson's patients (Cavanagh et al., in press).

In the response conflict task, RTs were tested in a 2 (information [EASY and HARD] vs. no-information [XXXX]) \times 2 (conflict: congruent vs. incongruent) generalized linear model. There were main effects for both information, $F(1,39) = 6.05$, $p < .05$, and conflict, $F(1,39) = 104.21$, $p < .001$, with no interaction, such that XXXX and incongruent trials had longer RTs. Error RTs did not differ from congruent RTs ($t < 1$). See Figure 2 for task performance means and standard errors.

Time–Frequency Results by Task and Condition

Figures 3 and 4 show stimulus- and response-locked EEG, with columns for each condition, and five rows each detailing different EEG features. All data are presented from the FCz electrode (except, of course, the topographic maps). The first row shows broadband (0.5–15 Hz) ERPs. The second row depicts theta-band (4–8 Hz)-filtered ERPs, showing consistent theta band phase-locking. The third and fourth rows show permutation thresholded power and intertrial phase coherence for each condition. All non-significant data have been omitted; thus, the colors on these time–frequency plots reflect statistically significant changes from rest. The bottom row shows the idiosyncratically scaled topographic plots of theta power (stimulus-locked: mean over 224–276 ms, response-locked: mean over –20–80 ms), demonstrating a consistent mid-frontal focus in nearly all conditions. Supplemental Figure 1 displays the broadband ERPs overlapped by condition. Although some plots show additional frontal and occipital regions that are active on these topoplots, Supplemental Figures 5–8 demonstrate that these are features of the average reference scheme, not contamination by artifact. Across reference schemes, there is a consistent mid-frontal focus of effect.

All stimulus- and response-locked conditions show a distinct pattern of theta power increase and phase consistency, although other findings outside the theta band are also worth noting here. A peri-response power decrease in the beta band is apparent in all trials requiring responses. The time–frequency plot of correct reinforcement feedback (Figure 3) is notable in that there is only a slight theta power enhancement, even though the theta ERP demonstrates consistent phase-locking and power increases. The error plot (Figure 4) shows a strong feature of delta band power and phase consistency that has been noted before (Yordanova et al., 2004). These features are discussed in greater detail in the discussion section. In sum, there was a strong and consistent theta power enhancement and phase consistency to all instances of stimulus and response processing.

Phase-Locked Theta: Comparison between Conditions

Theta-band-filtered ERPs were contrasted to formally test the proposed ubiquity of phase-locked theta across different conditions during stimulus processing or response commission. Figure 5 shows the theta-band-filtered ERPs from the second rows of Figures 3 and 4; however here they are overlapped with each task. The time window for the N2/FRN or CRN/ERN is indicated on each plot, demonstrating that ERP features that may be described under unique circumstances (i.e. “mismatch N2,” “FRN,” “control N2”) are all reflective of a highly similar underlying pattern of phase-locked theta band dynamics. Supplemental Figures 2–4

show the same ERP plots for delta (1–4 Hz), alpha (8–12 Hz), and beta (12–30 Hz) bands. Notably, these plots do not show a ubiquitous phase-locked feature across stimulus or response conditions, suggesting that these findings are not due to filter artifacts (cf. Yeung et al., 2007).

Figure 5c shows the between-condition phase consistency (PLV) for delta-, theta-, alpha-, and beta-band-filtered ERPs over time. In this application, the PLV quantifies the commonality of phase dynamics *between* conditions (as opposed to intertrial phase coherence, which acts between trials *within* a condition). The average theta PLV for stimuli (over 0–500 ms) was significantly higher than all other bands ($t_s > 3$, $p_s < .01$, Bonferroni corrected); the average theta PLV for responses (over –100–250 ms) was significantly higher than alpha and beta bands ($t_s > 2.4$, $p_s < .05$, Bonferroni corrected), but not different from the delta band ($t = 1$; we address this notable feature of delta phase coherence in the discussion). This finding quantifies how ERPs are composed of highly similar theta phases over time to all stimulus- and response-locked processes.

Time–Frequency Indices of Novelty, Conflict, Punishment, and Error

Data-driven differences between conditions are detailed in Figures 6 and 7. In the oddball task, both target and novel stimuli show increased mid-frontal theta band power and phase consistency compared to standards. In the reinforcement learning task, only punishment feedback showed an increase in power and phase consistency above its corresponding condition: There were no mid-frontal theta power increases at FCz due to conflict cues. In the response conflict task, noninformative cues elicited greater theta band power and phase consistency, whereas imperative cues elicited greater theta power and delta intertrial phase coherence. Figure 7 depicts the response-locked differences, where high-conflict responses and suboptimal choices on the reinforcement learning task failed to show notable theta power or intertrial phase coherence increases. This was a surprising outcome given previous ERP findings of reliably increased voltage negativities to suboptimal (Cavanagh, Gründler, Frank, & Allen, 2010; Frank et al., 2005; Gründler et al., 2009; Holroyd & Coles, 2002). In the response conflict task, both high-conflict (incongruent) and error conditions demonstrated theta power increases, with errors additionally characterized by delta power and intertrial phase coherence increases.

In the reinforcement learning task, conflict-related effects were also absent when each separate high-conflict condition (win–win and lose–lose) was compared to the low-conflict condition (win–lose). Additionally, there were no differences within or between high- and low-learning groups (defined by median or tertile splits based on test phase accuracy). In sum, mid-frontal theta power and phase coherence was specifically increased in conditions of novelty, punishment, and error, whereas conflict-related conditions varied in the extent and type of theta dynamic that was enhanced (or not). The additional contribution of delta power and intertrial phase coherence on error trials was strong and unique.

Contrasting ERP and Theta Power Measurements of Novelty, Conflict, Punishment, and Error

Three different methods were used to compare the performance of ERP and theta power measurements when resolving between-condition effects: (a) factor analysis, (b) planned comparisons, and

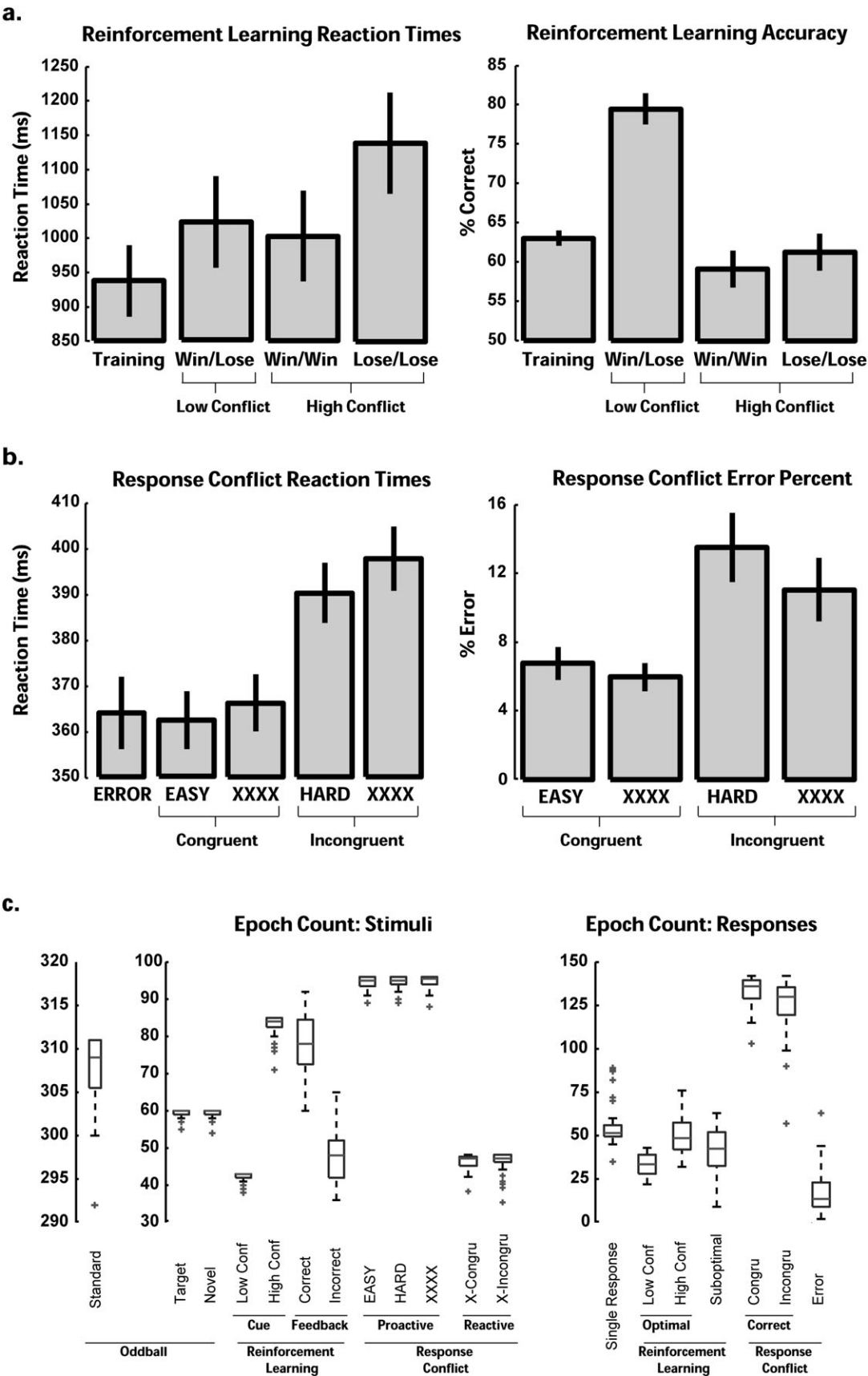


Figure 2. Performance and epoch count for EEG data. a: Reinforcement learning task: reaction time and accuracy. b: Response conflict task reaction time and accuracy. c: Boxplots of EEG epoch counts across participants for each condition.

Stimulus-Locked Activity

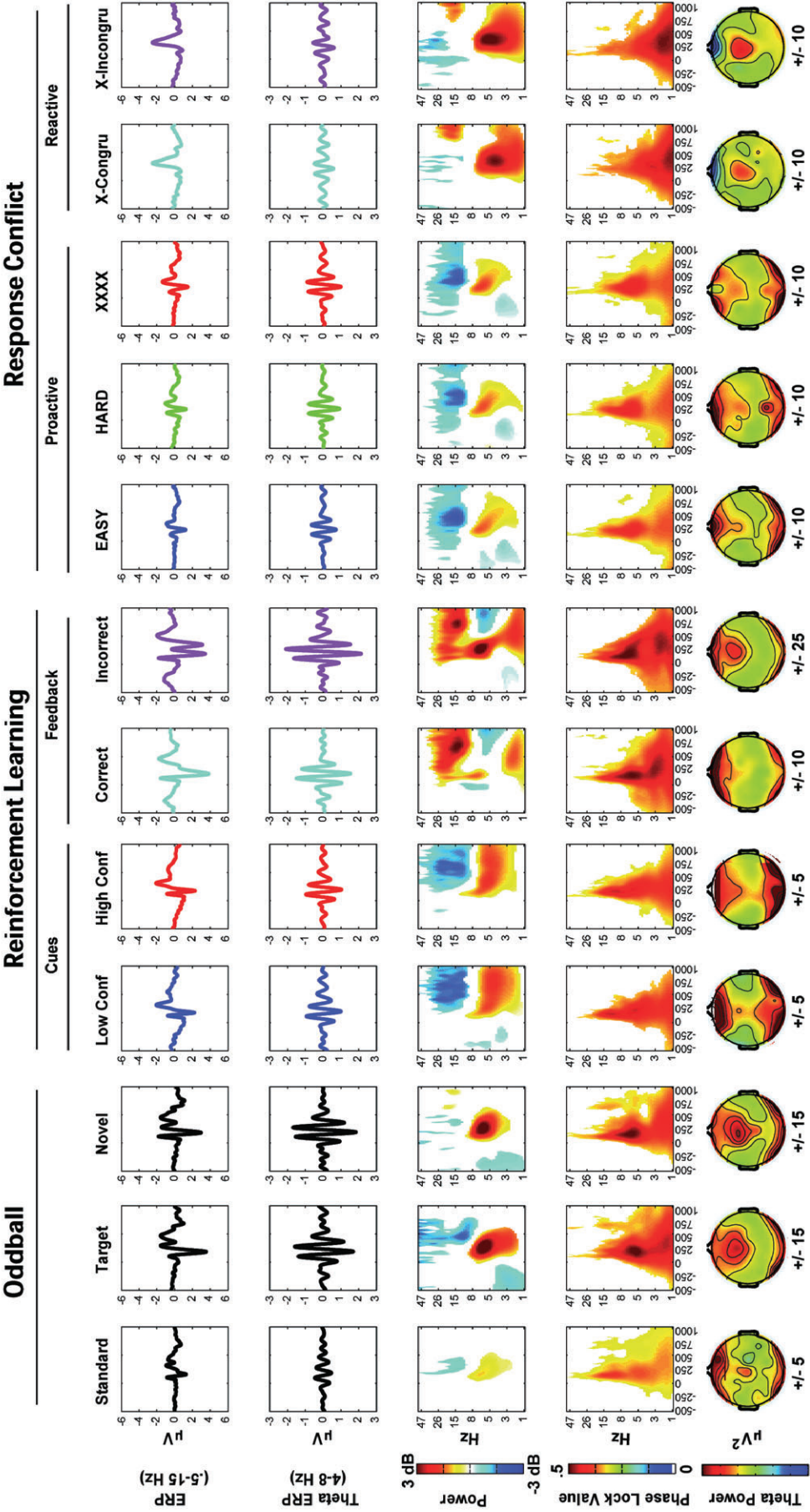


Figure 3. Stimulus-locked EEG at the FCz electrode. The first row shows standard ERPs; the second row demonstrates theta-band-specific phase-locked activities. The time-frequency plots show significant differences compared to rest (as revealed by permutation testing). Note the consistency of theta band power increases and phase consistency to all stimuli. Topomaps of theta power show mean activity from 224 to 276 ms postcue. Note the mediofrontal area: Although not strongly apparent in all topomaps, there is a consistent increase in theta power.

Response-Locked Activities

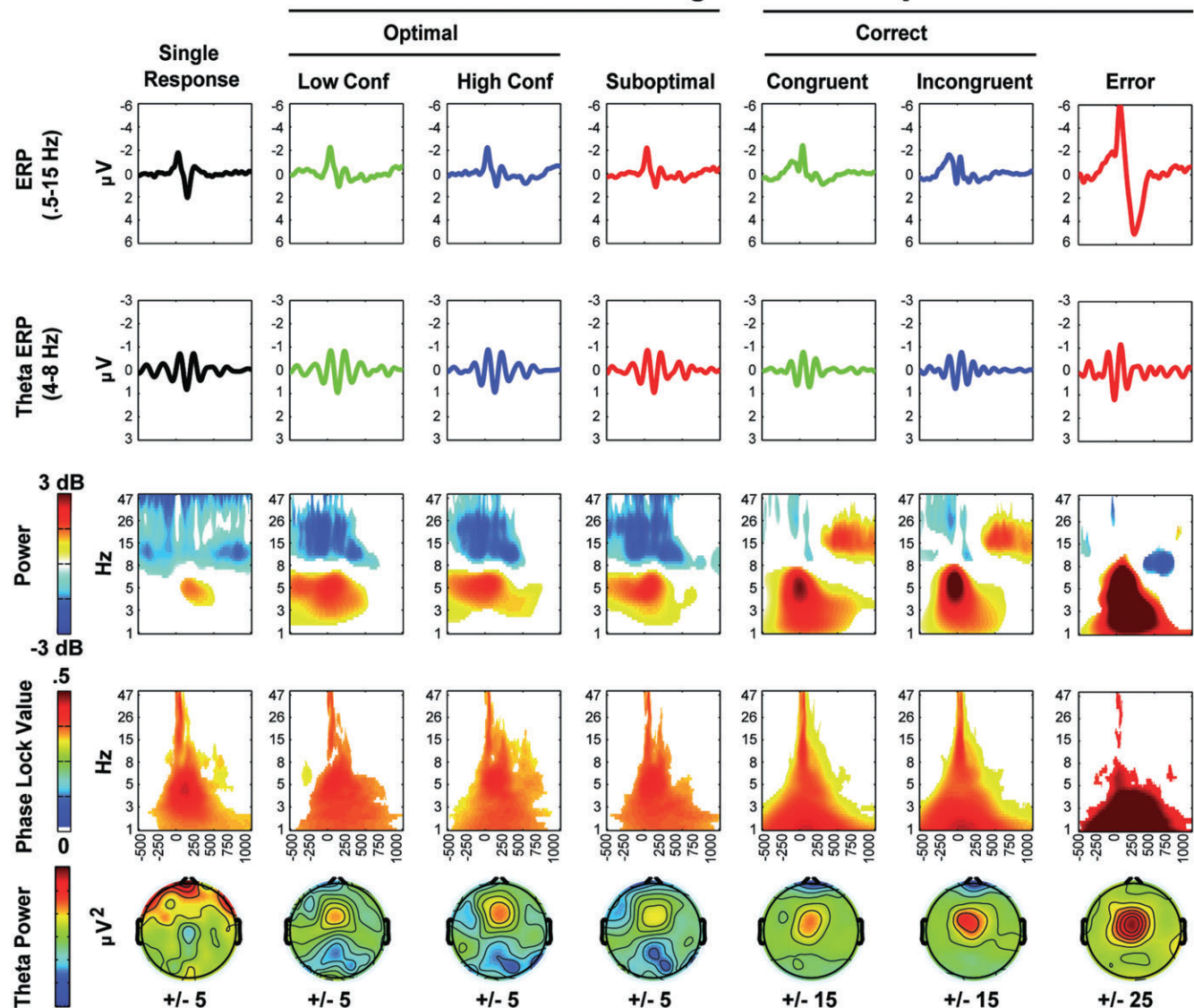


Figure 4. Response-locked EEG at the FCz electrode. The first row shows standard ERPs; the second row demonstrates theta-band-specific phase-locked activities. Time–frequency plots show significant differences compared to rest (as revealed by permutation testing). Note the consistency of theta power increases and phase consistency to all responses. Topomaps of theta power show mean activity from -20 to 80 ms peri-response. Note the mediofrontal area: There is a consistent increase in theta power.

(c) power analysis. First, to examine covariance of ERP and theta power measures, factor analyses were performed with both of these measurements included. In two separate factor analyses, the raw values and the difference measures from each respective contrast condition were examined, with similar results. For simplicity, the component loadings for the difference measures are detailed in Table 1 (Supplemental Table 2 details the raw data components). Table 1 demonstrates that there was considerable *between-measurement* covariation *within tasks*, particularly for oddball novelty, Simon response conflict and error, reinforcement learning punishment, and Simon task proactive conflict effects. Although factor loadings derived from a large number of variables with a

modest number of participants should be interpreted with caution, these findings provide additional evidence that theta power reflects the same variance as ERP measures to mid-frontal signals of novelty, conflict, punishment, and error.

Figure 8 contrasts theta power in decibels from the time–frequency plots (in gray) and peak–trough ERP amplitudes (in black) for each condition. The correlation between these measurements is shown behind the bars (in white), and lines underneath show significant a priori comparisons for novelty, conflict, punishment, and error. See Supplemental Table 1 for t test outputs. Whereas Figures 6 and 7 detail these same findings in the theta band, this plot demonstrates the functional similarity between

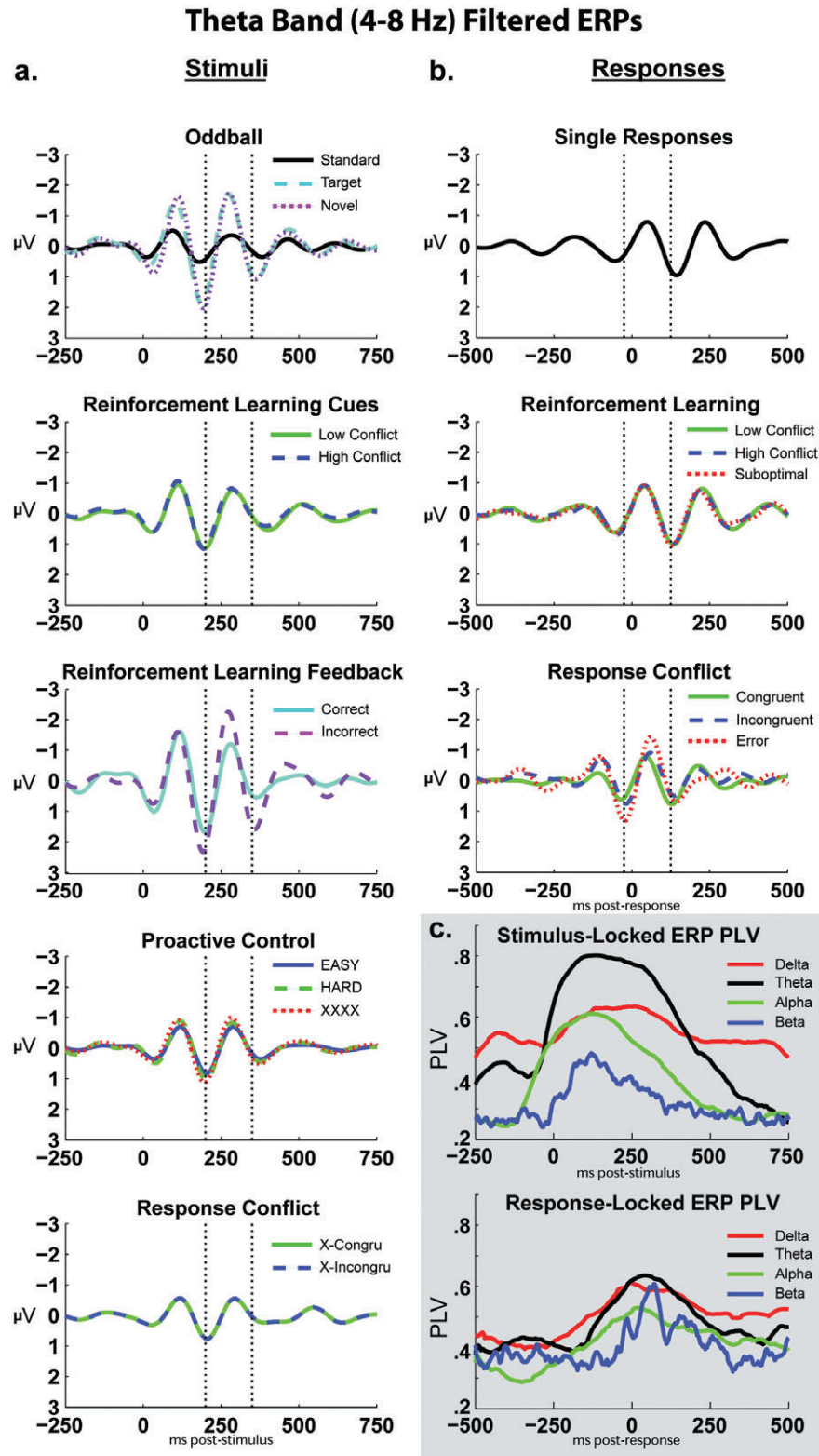


Figure 5. Theta band filtered ERPs at the FCz electrode, demonstrating the similarities between phase-locked power dynamics. a: Stimulus-locked trials: the time range of the N2/FRN component is shown in dashed vertical lines. b: Response-locked trials: the time range of the CRN/ERN is detailed in dashed vertical lines. c: Between-condition phase locking value of the band-filtered ERPs for stimuli and responses. These plots demonstrate how phase angles are remarkably consistent in the theta band following stimulus presentation and share a similar consistency with delta during response commission. See Supplemental Figures 2–4 for other band-filtered ERPs.

Stimulus-Locked Differences

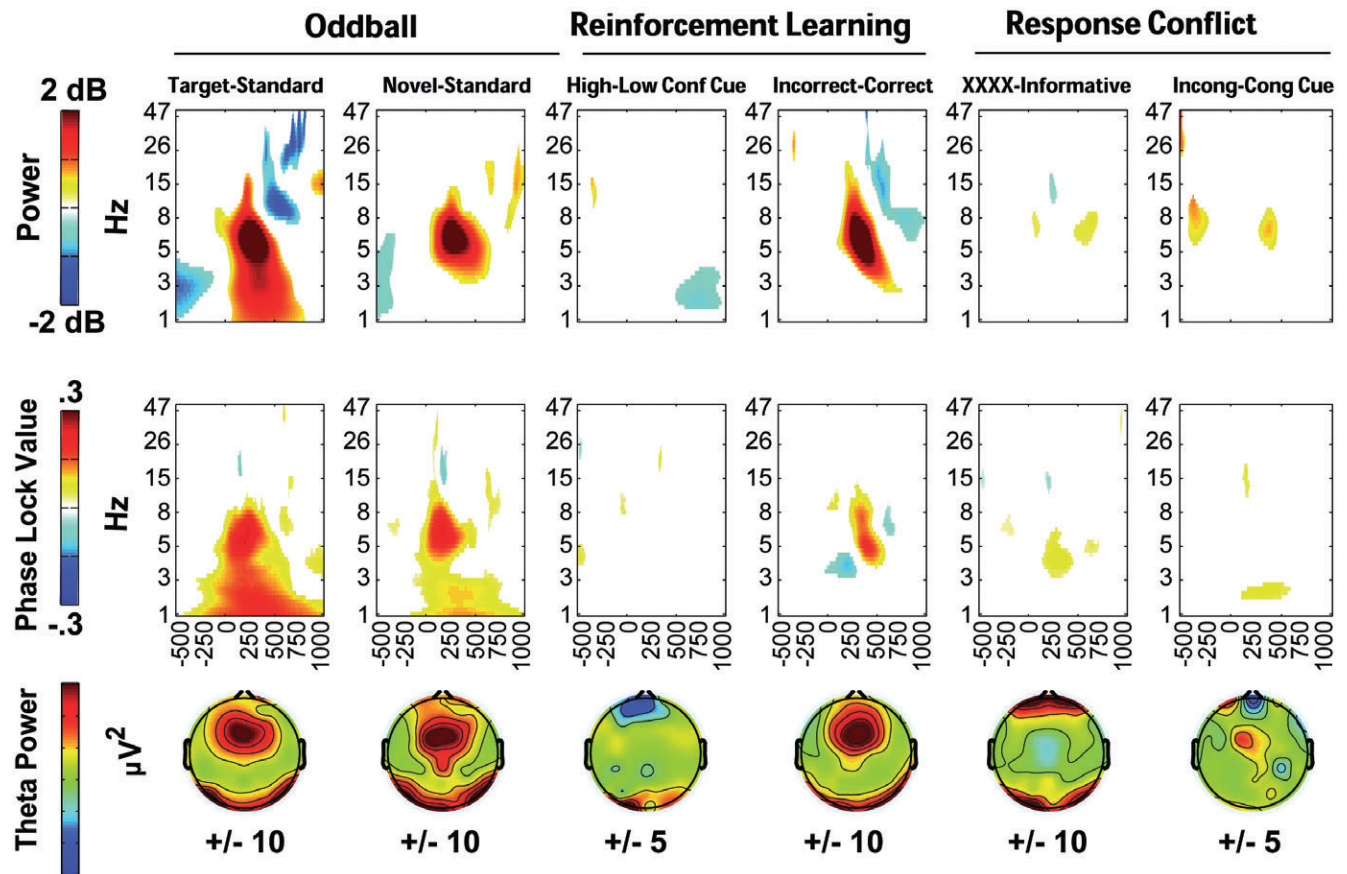


Figure 6. Cue-locked EEG differences in power and phase consistency at the FCz electrode. Time–frequency plots show significant differences between conditions (as revealed by permutation testing), demonstrating significant increases to novelty and punishment. Whereas cues in the reinforcement learning task did not have a significant power increase to conflict, proactive and reactive cues in the response conflict task show increased phase consistency and power, respectively. Topomaps of theta power show mean activity from 224 to 276 ms postcue. Note the increase of medio-frontal power to novelty and punishment on the topomaps. Conflict-related topoplots suggest that anterior regions may also contribute to differential processing.

standard ERP and theta power measurements in most, but not all conditions.³ The results of the power analyses are presented in Figure 9 and demonstrate that, in nearly every between-condition contrast, theta power had a larger effect size when compared to ERP amplitudes. When we summarize these analyses, it appears that theta power and ERP amplitude measurements similarly capture variance in action-monitoring processes, yet time–frequency measurements provide more information and a larger effect size. Together, the findings here suggest that theta dynamics are ubiquitous to stimuli and responses, and variance within this theta feature reflects neural responses due to novelty, conflict, punishment, and error.

Discussion

This study compared mid-frontal EEG activities during a wide variety of executive functions related to learning and performance

3. These contrasts were also performed with a mean amplitude measure of ERP power instead of the peak–trough difference, but the correlations were smaller in almost all cases.

(action monitoring). The ERP approach has defined psychologically relevant features of these EEG signals with varying initialisms (N2, FRN, ERN, CRN) based on timing, topography, and eliciting circumstances. Although this approach has led to a robust and differentiated literature of action-monitoring ERPs, this method may fail to communicate common features of these components. Fitting with the abundance of independent studies cited in the Introduction, the current study suggests that mid-frontal theta is the dominant characteristic of all of these aforementioned ERP components. This commonality has important implications for interpreting the functional and computational roles of these scalp-recorded signals.

Theta: Consistency and Enhancement

Figures 3 and 4 clearly demonstrate a similar theta band feature during stimulus processing and motor responses. While there is also significant activity in other frequency bands, there are no other band-specific phenomena that are so consistent across conditions. Topographic maps of theta power detail a variety of cortical areas that are active during stimulus and response processing, yet there is

Response-Locked Differences

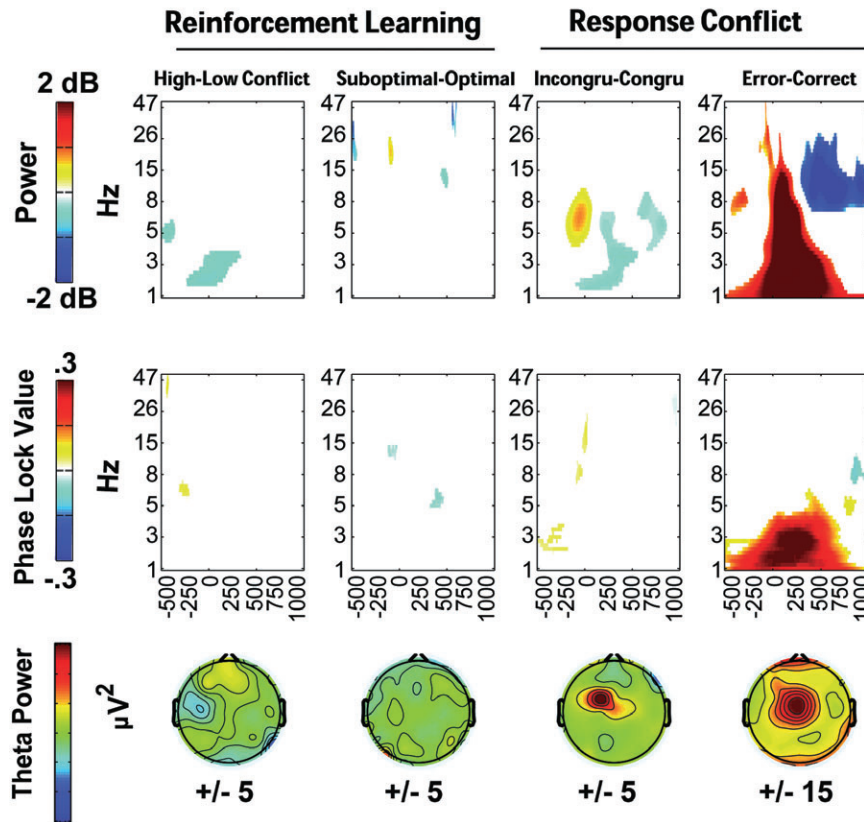


Figure 7. Response-locked EEG differences in power and phase consistency at the FCz electrode. Time–frequency plots show significant differences between conditions (as revealed by permutation testing), demonstrating significant increases to conflict and error in the response conflict task. In the reinforcement learning task, conflict and error responses did not have a similar profile of significantly increased theta power. Topomaps of theta power show mean activity from –20 to 80 ms postcue. Note the increase of medio-frontal power to conflict and error.

a reliable mid-frontal focus of activity. Phase-locked theta ERPs and the dominance of theta band power and intertrial phase coherence in the time–frequency representations suggest that this specific frequency band contributes strongly to mid-frontal ERP components (the stimulus-locked P2-N2 complex and the response-locked ERN/CRN). The strong theta band ERP phase consistency between conditions (Figure 5c) suggests that a similar phase-locked feature is shared between conditions. These findings provide evidence that this specific frequency and phase dynamic may reflect a common mechanism for temporal organization of neural processes during action monitoring.

Figures 6 and 7 demonstrate that mid-frontal theta power is enhanced in conditions of novelty, conflict, punishment, and error. In fact, mid-frontal theta and standard ERP measures were both similarly modulated by these factors (Figure 8). Although there were slight differences in statistical significance that might reflect meaningful benefits of one method over the other in certain circumstances (ERP measures differentiated target and novel oddball conditions and proactive conflict Simon task conditions; theta power differentiated stimulus and response conflict during the Simon task), both measures reliably reflected the experimental conditions of novelty, conflict, punishment, and error. Even the unexpected failures to replicate previous findings

(suboptimal > optimal responses in reinforcement learning)⁴ and to differentiate novel conditions (high vs. low conflict in stimulus- and response-locked reinforcement learning conditions) were common to both theta and ERP methods. These findings suggest that, in addition to the dominant and shared theta band basis of the ERPs, both measures reflect the same psychologically meaningful constructs. This interpretation is supported by the factor analysis, which demonstrated that ERP and theta measures covary during novelty, conflict, punishment, and error processes. Yet, the power analyses (Figure 9) suggests that theta power may be a more sensitive index of between-condition differences than ERP amplitudes. Although each measurement approach has methodological advantages and disadvantages, interpretation of these signals in the context of a common theta band process offers the most parsimonious and powerful explanation of function. An appreciation of the common theta band process underlying these diverse features may offer theoretical and practical advantages.

4. We suspect that the failure to replicate suboptimal > optimal differences may be due to the short and simple blocks of this reinforcement learning task compared to other tasks with demonstrated successful replications (Cavanagh, Gründler, et al., 2010; Frank et al., 2005; Gründler et al., 2009; Holroyd & Coles, 2002).

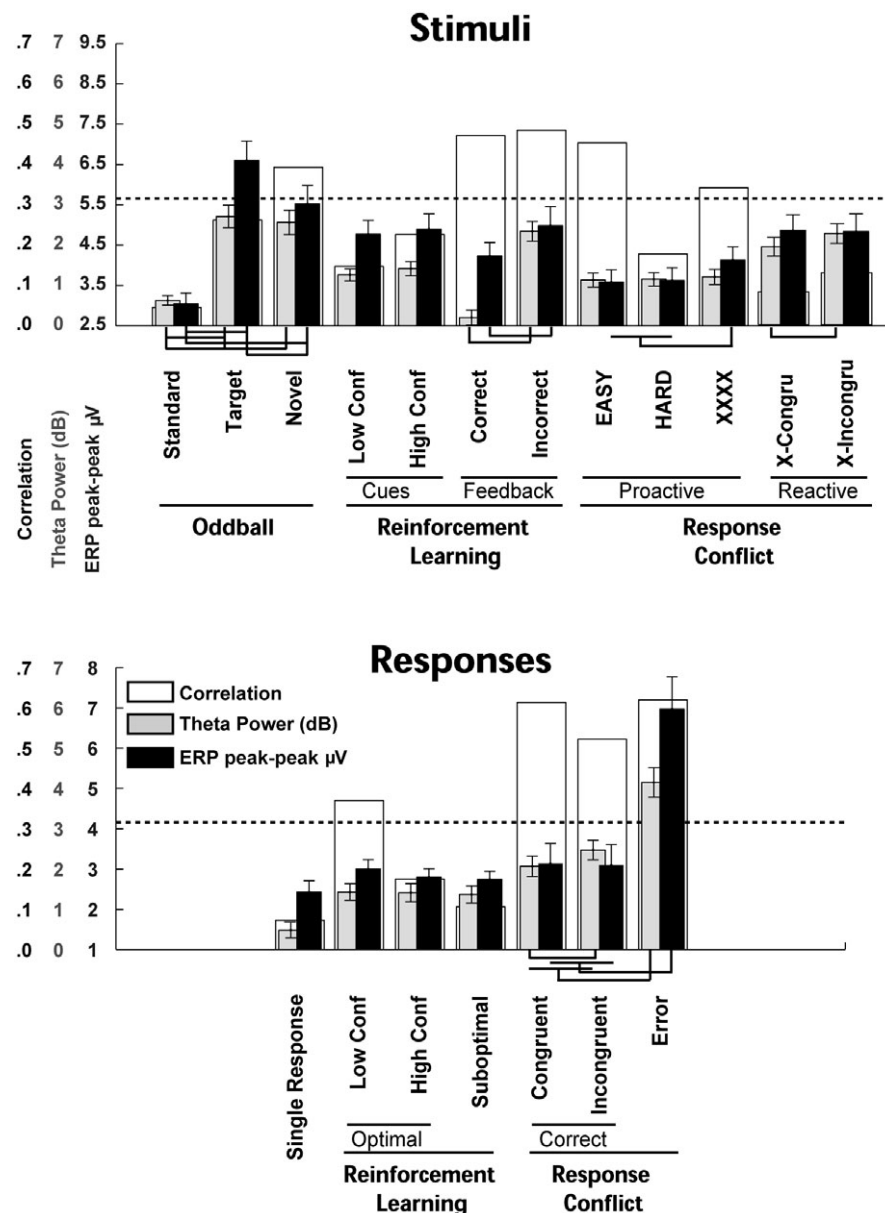


Figure 8. ERP amplitudes (μV) and theta power (dB) for each condition. Stimulus-locked components were measured to capture variance in the N2/ERN time range. Response-locked components capture variance in the CRN/ERN time range. Note the three scales on the ordinate: ERP μV (offset for scaling purposes), theta power (dB), and the correlation between the two. Correlations between ERP and theta values are shown behind the bar plots for each condition; the horizontal dashed line shows the significance threshold. Under each bar plot, a priori t tests between ERPs and theta power values show significant increases due to novelty, proactive conflict (ERP only), reactive conflict (theta only), punishment, and error. Although there were no significant conflict-related increases to stimuli or responses on the reinforcement learning task, null effects are mirrored by both ERP and theta power measures.

A Theoretical Role of Theta Dynamics

Here we examine the hypothesis that mid-frontal theta phase dynamics act as common templates for the temporal organization of neural responses to stimuli and responses, with variation on this template reflecting neural reactions to novelty, conflict, punishment, and error. EEG dynamics reflect physiological mechanisms for organizing and communicating neural computations. Synchronous oscillations are thought to reflect a mechanism for entrained interregional activity: Rhythmic excitability may allow temporal windows of coordinated spike timing across spatially separate neural networks, presumably reflecting functional com-

munication (Buzsáki, 2006; Buzsáki & Draguhn, 2004; Fries, 2005; Womelsdorf et al., 2007). The ubiquity of theta band findings across species has led to the suggestion that theta reflects a non-specific mechanism for organizing neural processes around “decision points,” such as action selection (Womelsdorf, Vinck, Leung, & Everling, 2010). The high degree of intertrial and cross-condition theta phase consistency reported here provides evidence that these theta activities to stimuli and responses reflect a common template for the temporal organization of neuronal populations during endogenous and exogenous action-monitoring processes. Novelty, conflict, punishment, and error responses all appear to be primarily indicated by power increases on this common organiza-

Table 1. Factor Analysis Output of Difference Scores for Both EEG Measurements (Theta Power and ERP Amplitude) Highlighting Novelty, Conflict, Punishment, and Error

Component	Varimax Loading													
	1		2		3		4		5		6		7	
Measurement (theta or ERP)	T	E	T	E	T	E	T	E	T	E	T	E	T	E
% variance	18%		12%		10%		9%		7%		7%		6%	
Target – standard stim	0.85	0.49					0.39	0.62						
Novel – standard stim	0.81	0.55					0.00	0.40						
High – low conflict stim			0.36				0.58				0.61		–0.33	
Incorrect – correct stim					0.66	0.31	0.38							0.64
XXXX: (EASY & HARD) stim	0.43				–0.61						0.35	0.87		
Incongruent – congruent cue stim			0.61				–0.44			0.79			0.32	
High – low conflict response				0.38			–0.44	0.36					0.74	
Suboptimal – optimal response					–0.66		–0.77							
Incongruent – congruent response		–0.52	0.69	0.37	–0.39				–0.48					
Error – correct response			0.77	0.72										

Note. There is considerable between-measurement shared variance for oddball novelty effects (Component 1), Simon task response conflict and errors (Component 2), reinforcement learning task punishment (Component 3), and Simon task proactive conflict cues (Component 6). Other components appear to reflect within-measurement variance (Components 4 and 5) and an undetermined cluster (Component 7).

tional theme. We qualify this simplification by noting that there are slight frequency and phase differences between conditions (Figure 5), and experimental factors also elicit changes in theta phase dynamics and have varied contributions from other frequency bands (Figures 6 and 7). However, here we aim to distinguish broad effects and commonalities between conditions.

The current study demonstrated that simple button presses—where only a digit on one hand is capable of executing the required action—evoke an event-related theta band power increase and phase consistency that is reflected in the ERP as a negative deflection (i.e., the CRN). This suggests that this theta response to motor selection is a reflection of a generic process of mPFC functioning: The act of making a single motor response without the possibility of response conflict (as traditionally defined) produces the theta/CRN feature. Similarly, an event-related theta/N2 dynamic is elicited by the standard stimuli in the oddball task (observing a standard visual stimulus). This pattern suggests that *generic* event-related endogenous and exogenous processes may be reflected by theta band dynamics in the time range of the ERN/CRN and the FRN/N2, respectively.

Experimental factors can cause dissociation in ERP component amplitudes between conditions, as do lesions (Gehring & Knight, 2000; Swick & Turken, 2002; Ullsperger & von Cramon, 2006), drug challenge (de Bruijn, Hulstijn, Verkes, Ruigt, & Sabbe, 2004; de Bruijn, Sabbe, Hulstijn, Ruigt, & Verkes, 2006; Zirnheld et al., 2004), and even clinical symptomatology (Gründler et al., 2009). However, the basic morphology of relevant stimulus and response ERP components were retained in all of these cases, in line with the idea of common templates. It should be noted that this hypothesis of temporal organization is lacking in spatial specificity beyond the single electrode (FCz) reported here. Different conditions likely reflect an aggregation of multiple contributing sources (cf. Cohen et al., 2008). Indeed, distributed sources may be ideally served by a common, low-frequency temporal organizational scheme.

Practical Implications for Event-Related EEG

Novel analysis methods that are well suited to time–frequency methods, including single-trial analysis, can reveal more information than the standard fixed effect analysis reported here (Cohen,

2011). As an example of a benefit of time–frequency analytic perspective, consider the EEG response to correct reinforcement feedback. The neural response to correct feedback was characterized by a very slight degree of theta power increase above rest (Figure 3). This finding fits with the description of a reward positivity ERP component that has been suggested to “cancel out” the N2 component (Baker & Holroyd, 2011; Holroyd et al., 2008); see the Figure 3 broadband ERP at ~250–500 ms. Although theta power was diminished during correct feedback trials, the phase-locked theta ERP and strong theta phase consistency demonstrate that the common theta phase dynamic to stimulus processing remained intact, contributing to the evidence that this theta response reflects a common temporal template. Future investigations will need to determine what part of the N2/theta process to rewards is canceled, diminished, or overlapped by other processes: The current findings suggest that phase-related activities are retained, yet power-related activities are diminished during positive reinforcement.

Another benefit of time–frequency description of event-related EEG may be a more careful summary of possibly related events. For example, the error-following Pe component (Overbeek, Nieuwenhuis, & Ridderinkhof, 2005) is often parsed into an early mid-frontal positivity (~250 ms post-error; see Figure 4, row 1, column 5) and a late posterior positivity (~400–500 ms post-error; Van Veen & Carter, 2002). Yet, the morphology of the early Pe appears to be the peak of the theta/delta deflection immediately following the ERN. Although this EEG feature may reflect a psychologically unique construct that is not reflected in the ERN, it may also be a reflection of the next (180°) peak of the theta or delta process. A similar argument could be made about the P3a to novel stimuli: Many of the voltage negativities in the N2 time range reflect parts of multiphasic waveforms that have been associated with a temporal cascade of mismatch processing. Huster, Westerhausen, Pantev, and Konrad (2010) reviewed a number of source localization studies of the N2 and P3 in response inhibition tasks and demonstrated that these components were associated with anterior and posterior midcingulate activation, respectively, each within a unique network of other brain activations. However, the scope of this investigation did not aim to define later, related ERP components or other components potentially associated with theta activi-

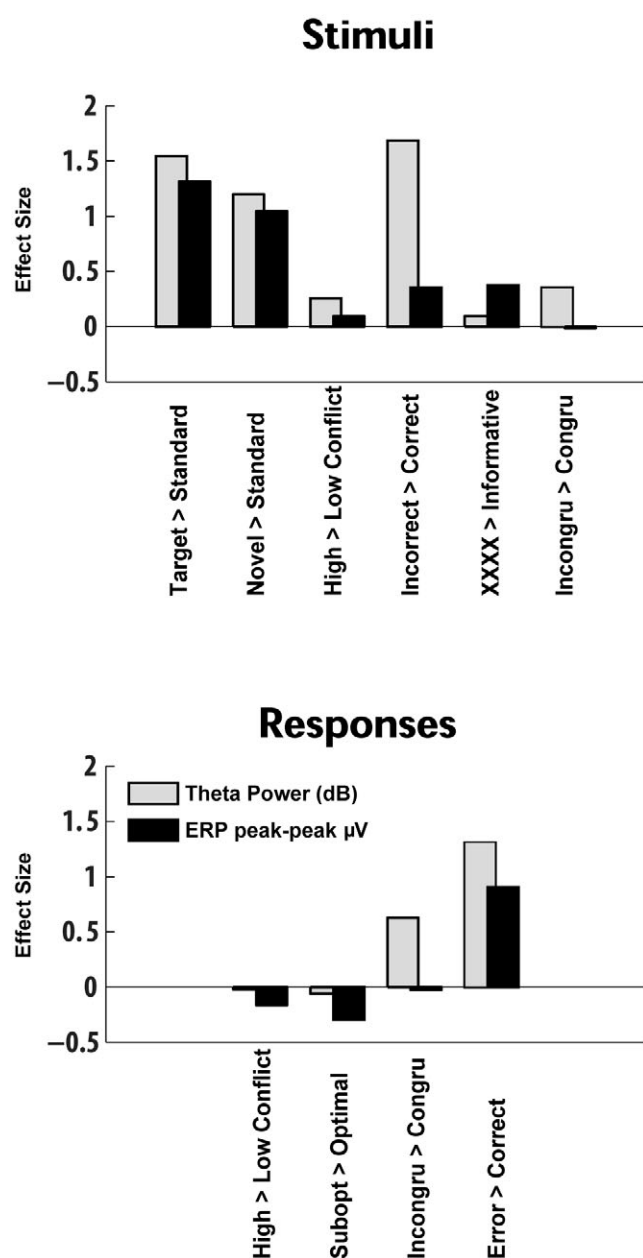


Figure 9. Effect size of novelty, conflict, punishment, and error for ERP components and theta power. In nearly all cases, theta power had a larger effect size for these events.

ties to mismatch or control (i.e., mismatch negativity, stop signal N2, no-go N2). In sum, these examples demonstrate that without an appreciation of common underlying temporal-spectral features, the ERP literature may suffer from a lack of parsimonious accounting of neural responses.

Delta and Beta Bands

Before moving on to further discussion of the relevance of theta band dynamics, findings in other frequency bands are addressed. Besides the common theta feature, each time-frequency representation showed unique temporal, spatial, and frequency effects, detailing a multitude of condition-specific patterns. There was

consistent beta band power suppression before, during, and after motor responses. This consistent beta power decrease to manual responses (sometimes termed desynchronization or beta blocking) stands in contrast to the notable beta power enhancement following performance feedback (Figure 3). Replicating previous findings (Cohen et al., 2007; Marco-Pallares et al., 2008), beta power was greater following correct than incorrect feedback (the inverse pattern is shown in Figure 7), even though this finding has not been consistently replicated (Cavanagh, Frank, et al., 2010; Christie & Tata, 2009). A functional interpretation of this feedback-specific beta response remains to be defined, although some have suggested that mediofrontal-motor cortex coactivity is increased following feedback (Cohen & Ranganath, 2007).

Delta band power increases were apparent during demanding motor responses on the response conflict task, and they were especially prevalent on errors (also see Yordanova et al., 2004). Delta activity could reflect error-specific processing in mPFC, the combined summation of other neural areas that contribute specifically to errors, or even variance traditionally associated with the Pe. Delta and theta bands were equally phase coherent during responses (Figure 5c), and all frequency bands increased in phase consistency immediately following a response. Although these findings do not argue against a special role for theta band dynamics, they do indicate that there are a multitude of interactive processes during manual responses. Dissociation among these frequency band effects may reveal unique computational functions. For example, although responses are associated with strong theta and delta intertrial phase coherence, only theta phase dynamics are relevant to conflict-related RT adaptation (Cohen & Cavanagh, 2011), fitting with other findings that theta power predicts RT adaptation following conflict (Cavanagh et al., in press), punishment (Cavanagh, Frank, et al., 2010), and error (Cavanagh et al., 2009; Debener et al., 2005).

A Generic Reflection of Cortical Processing

It is important to note that neither the mPFC nor the field of action monitoring is unique in regard to theta band reflections of active processing. Human cortical theta is generated from multiple local sites (Caplan et al., 2003; Jacobs, Hwang, Curran, & Kahana, 2006; Raghavachari et al., 2006), but the specific case of frontal midline theta has been localized to the ACC and surrounding mPFC areas using magnetoencephalography (Ishii et al., 1999) and EEG (Gevins & Smith, 2000; Gevins, Smith, McEvoy, & Yu, 1997; Gevins, Smith, McEvoy, Leong, & Le, 1999; Jensen & Tesche, 2002; Onton et al., 2005). Cortical theta has been broadly implicated in sensorimotor integration during spatial navigation (Baker & Holroyd, 2009; Caplan et al., 2003) and episodic memory encoding and retrieval (Jacobs et al., 2006; Kahana, Sekuler, Caplan, Kirschen, & Madsen, 1999; Klimesch, 1999; Klimesch, Doppelmayr, Schwaiger, Winkler, & Gruber, 2000; Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007; Nyhus & Curran, 2010; Raghavachari et al., 2006; Rizzuto, Madsen, Bromfield, Schulze-Bonhage, & Kahana, 2006; Rizzuto et al., 2003; Sauseng et al., 2004), and the specific case of frontal midline theta has been implicated in decision making and working memory maintenance (Gevins et al., 1997; Ishii et al., 1999; Onton et al., 2005; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010). Recent studies have begun to identify how mPFC operations implicated in adaptive control may specifically contribute to these other cognitive phenomena, including conflict processing during memory retrieval (Hanslmayr, Staudigl, Aslan, & Bauml, 2010; Staudigl, Hanslmayr, & Bauml, 2010) and effortful attention during decision making

(Mulert, Menzinger, Leicht, Pogarell, & Hegerl, 2005; Mulert et al., 2008). These functional and topographic distinctions further demonstrate how theta band power dynamics likely reflect a non-specific marker of active cortical operation. In this article, we only address event-related mid-frontal theta responses during action-monitoring tasks. It is likely that other investigations will reveal unique and dissociated functions of cortical theta to a variety of cognitive processes.

Implications for Theories of ERP Responses

Most theoretical or computational accounts of the ERN, FRN, and N2 ERPs involve a comparator function. The ERN has been suggested to reflect a comparison between correct versus actual motor responses (perhaps using an afferent motor copy; Coles, Scheffers, & Holroyd, 2001; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). In reinforcement learning, both the ERN and FRN have been suggested to reflect negative reward (punishment) prediction errors (Holroyd & Coles, 2002), as defined by reinforcement learning theory (Sutton & Barto, 1998). The eponymous mismatch N2 implies a perceptual difference between actual experience and past history or predominant category (Folstein & Van Petten, 2008), whereas the control N2 appears to be related to the occurrence of conflict, which may be more broadly defined. One common definition of conflict stands out from the comparator description: the Yeung, Botvinick, et al. (2004) model of the ERN and conflict N2 does not invoke a comparison per se, but rather interprets the degree of coactivity between motor preparations as conflict (Hopfield, 1982). Although these influential theories may appear to suggest functional differences, one can also highlight computational similarities between mismatch comparison and measures of coactivity such as free energy or entropy (Friston, 2003, 2005; O'Reilly & Munakata, 2000).

One notable exception to these theoretical accounts involves the CRN, which is not specifically accounted for in any major theories of human action monitoring and which may not involve a comparator function or even coactive motor responses. If the CRN is interpreted as an inherent feature of theta band phase activities during manual responses, as highlighted by the single response task response-locked theta, previous theoretical and computational accounts (mismatch or conflict) of the ERN may still be considered accurate accounts of enhanced processes that take place over an inherent background of phase-locked theta dynamics. As these theories and models continue to integrate and evolve (see Cockburn & Frank, 2011; Holroyd & Yeung, 2011), inclusion of such biophysical details will contribute to the biological realism and accurate empirical verification of future model-based predictions.

Implications for Theories of ACC

Computational models of general ACC function have suggested this neural system acts as an evaluative node in a global computational workspace (Botvinick et al., 2001; Dehaene, Kerszberg,

& Changeux, 1998), especially when effort and vigilance are required. In both these models, errors increase vigilance and connectivity between distributed processing nodes, which then decline again as the task becomes routine—eventually leading to more errors. This account suggests that a low-level, basic monitoring process underlies action monitoring and that errors function as alarm signals when the task is not being performed as expected. Theta dynamics appear to reflect the operations of this hypothesized ACC node.

Novelty, conflict, punishment, and error could all be considered signals that increase vigilance and active processing (which may be defined as surprise, effort, or attention in some cases). Microelectrode recordings in dorsal ACC reflect theta dynamics in the same microdomain to different tasks and stimuli, including errors, novelty, and effortful processing (Wang et al., 2005), fitting with other invasive recordings across species (Cohen et al., 2008; Leung & Borst, 1987; Tsujimoto et al., 2006; Womelsdorf, Johnston, Vinck, & Everling, 2010). A decline in EEG power has also been detailed in CRNs/theta power (Cavanagh et al., 2009; Vidal et al., 2000, 2003) and N2s (Eichele, Juvodden, Ullsperger, & Eichele, 2010) immediately prior to an error. Following an event, transient theta phase relations between mid-frontal and other brain areas have been proposed to reflect a communication mechanism for vigilance-instantiated cognitive control with lateral PFC (Cavanagh et al., 2009; Cavanagh, Frank, et al., 2010; Cohen & Cavanagh, 2011; Hanslmayr et al., 2008), and sensory attention with the occipital lobe (Cohen, van Gaal, Ridderinkhof, & Lamme, 2009). Widespread intracranial phase synchrony between ACC and other sites has been detailed as well, to multiple types of eliciting stimuli (Wang et al., 2005). Given that both ERN amplitudes and ACC activities are modulated by negative affect and anxious arousal (Etkin, Egner, & Kalisch, 2011; Olvet & Hajcak, 2008; Shackman et al., 2011), theta appears to be a sensitive index of multidimensional aspects of mPFC function.

Conclusion

A common language can be used to communicate many different things. The ubiquity of mid-frontal theta suggests that this signal reflects a generic processing mechanism for coordinating endogenous and exogenous performance-relevant information. This process is enhanced in situations typically associated with mPFC functioning: reactive responses to novelty, conflict, punishment, and error. Theta band phase dynamics may represent a biophysical mechanism for the common temporal organization of neural processes during stimulus or response processes. Variation on this theme, such as power enhancement, appears to reflect the realization of these reactive responses. These computations appear to be used to merge attentive, affective, and cognitive functions with motor selection in order to utilize environmental context during action monitoring. Theta therefore appears to reflect general operations of the mPFC during action monitoring.

References

- Baker, T. E., & Holroyd, C. B. (2009). Which way do I go? Neural activation in response to feedback and spatial processing in a virtual T-maze. *Cerebral Cortex*, 19, 1708–1722. doi: 10.1093/cercor/bhn223
- Baker, T. E., & Holroyd, C. B. (2011). Dissociated roles of the anterior cingulate cortex in reward and conflict processing as revealed by the feedback error-related negativity and N200. *Biological Psychology*, 87, 25–34. doi: 10.1016/j.biopsycho.2011.01.010
- Bernat, E. M., Nelson, L. D., Holroyd, C. B., Gehring, W. J., & Patrick, C. J. (2008). Separating cognitive processes with principal components analysis of EEG time–frequency distributions. *Proceedings of the SPIE*, 7074, 70740S–70740S-10.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, 108, 624–652.

- Burle, B., Roger, C., Allain, S., Vidal, F., & Hasbroucq, T. (2008). Error negativity does not reflect conflict: A reappraisal of conflict monitoring and anterior cingulate cortex activity. *Journal of Cognitive Neuroscience*, 20, 1637–1655. doi: 10.1162/jocn.2008.20110
- Buzsáki, G. (2006). *Rhythms of the brain*. Oxford: Oxford University Press.
- Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science*, 304, 1926–1929. doi: 10.1126/science.1099745
- Caplan, J. B., Madsen, J. R., Schulze-Bonhage, A., Aschenbrenner-Scheibe, R., Newman, E. L., & Kahana, M. J. (2003). Human theta oscillations related to sensorimotor integration and spatial learning. *Journal of Neuroscience*, 23, 4726–4736.
- Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, 280, 747–749.
- Cavanagh, J. F., Cohen, M. X., & Allen, J. J. (2009). Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. *Journal of Neuroscience*, 29, 98–105. doi: 10.1523/JNEUROSCI.4137-08.2009
- Cavanagh, J. F., Frank, M. J., Klein, T. J., & Allen, J. J. B. (2010). Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. *NeuroImage*, 49, 3198–3209.
- Cavanagh, J. F., Gründler, T. O. J., Frank, M. J., & Allen, J. J. B. (2010). Altered cingulate sub-region activation accounts for task-related dissociation in ERN amplitude as a function of obsessive-compulsive symptoms. *Neuropsychologia*, 48, 2098–2109. doi: 10.1016/j.neuropsychologia.2010.03.031
- Cavanagh, J. F., Wiecki, T. V., Cohen, M. X., Figueroa, C., Samanta, J., Sherman, S. J., & Frank, M. J. (in press). Subthalamic nucleus stimulation reverses mediofrontal influence over decision threshold. *Nature Neuroscience*.
- Christie, G. J., & Tata, M. S. (2009). Right frontal cortex generates reward-related theta-band oscillatory activity. *NeuroImage*, 48, 415–422. doi: 10.1016/j.neuroimage.2009.06.076
- Cockburn, J., & Frank, M. (2011). Reinforcement learning, conflict monitoring, and cognitive control: An integrative model of cingulate-striatal interactions and the ERN. In R. Mars, J. Sallet, M. Rushworth, & N. Yeung (Eds.), *Neural basis of motivational and cognitive control* (pp. 311–331). Cambridge, MA: MIT Press.
- Cohen, M. X. (2011). It's about time. *Frontiers in Human Neuroscience*, 5, 2. doi: 10.3389/fnhum.2011.00002
- Cohen, M. X., & Cavanagh, J. F. (2011). Single-trial regression elucidates the role of prefrontal theta oscillations in response conflict. *Frontiers in Psychology*, 2, 1–12.
- Cohen, M. X., Elger, C. E., & Ranganath, C. (2007). Reward expectation modulates feedback-related negativity and EEG spectra. *NeuroImage*, 35, 968–978. doi: 10.1016/j.neuroimage.2006.11.056
- Cohen, M. X., & Ranganath, C. (2007). Reinforcement learning signals predict future decisions. *Journal of Neuroscience*, 27, 371–378. doi: 10.1523/JNEUROSCI.4421-06.2007
- Cohen, M. X., Ridderinkhof, K. R., Haupt, S., Elger, C. E., & Fell, J. (2008). Medial frontal cortex and response conflict: Evidence from human intracranial EEG and medial frontal cortex lesion. *Brain Research*, 1238, 127–142. doi: 10.1016/j.brainres.2008.07.114
- Cohen, M. X., van Gaal, S., Ridderinkhof, K. R., & Lamme, V. A. (2009). Unconscious errors enhance prefrontal-occipital oscillatory synchrony. *Frontiers in Human Neuroscience*, 3, 54. doi: 10.3389/fnhum.2009.0054
- Coles, M. G., Scheffers, M. K., & Holroyd, C. B. (2001). Why is there an ERN/Ne on correct trials? Response representations, stimulus-related components, and the theory of error-processing. *Biological Psychology*, 56, 173–189.
- de Bruijn, E. R., Hulstijn, W., Verkes, R. J., Ruigt, G. S., & Sabbe, B. G. (2004). Drug-induced stimulation and suppression of action monitoring in healthy volunteers. *Psychopharmacology*, 177, 151–160. doi: 10.1007/s00213-004-1915-6
- de Bruijn, E. R., Sabbe, B. G., Hulstijn, W., Ruigt, G. S., & Verkes, R. J. (2006). Effects of antipsychotic and antidepressant drugs on action monitoring in healthy volunteers. *Brain Research*, 1105, 122–129. doi: 10.1016/j.brainres.2006.01.006
- Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., von Cramon, D. Y., & Engel, A. K. (2005). Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. *Journal of Neuroscience*, 25, 11730–11737. doi: 10.1523/JNEUROSCI.3286-05.2005
- Dehaene, S., Kerszberg, M., & Changeux, J. P. (1998). A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences, USA*, 95, 14529–14534.
- 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. doi: 10.1016/j.jneumeth.2003.10.009
- Devinsky, O., Morrell, M. J., & Vogt, B. A. (1995). Contributions of anterior cingulate cortex to behaviour. *Brain*, 118, 279–306.
- Donkers, F. C., Nieuwenhuis, S., & van Boxtel, G. J. (2005). Mediofrontal negativities in the absence of responding. *Brain Research, Cognitive Brain Research*, 25, 777–787. doi: 10.1016/j.cogbrainres.2005.09.007
- Donkers, F. C., & van Boxtel, G. J. (2004). The N2 in go/no-go tasks reflects conflict monitoring not response inhibition. *Brain and Cognition*, 56, 165–176. doi: 10.1016/j.bandc.2004.04.005
- Eichele, H., Juvodden, H. T., Ullsperger, M., & Eichele, T. (2010). Mal-adaptation of event-related EEG responses preceding performance errors. *Frontiers in Human Neuroscience*, 4. doi: 10.3389/fnhum.2010.00065
- Etkin, A., Egner, T., & Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Sciences*, 15, 85–93. doi: 10.1016/j.tics.2010.11.004
- Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. *Electroencephalography and Clinical Neurophysiology*, 78, 447–455.
- Falkenstein, M., Hoormann, J., Christ, S., & Hohnsbein, J. (2000). ERP components on reaction errors and their functional significance: A tutorial. *Biological Psychology*, 51, 87–107.
- Fell, J., Dietl, T., Grunwald, T., Kurthen, M., Klaver, P., Trautner, P., . . . Fernández, G. (2004). Neural bases of cognitive ERPs: More than phase reset. *Journal of Cognitive Neuroscience*, 16, 1595–1604. doi: 10.1162/0898929042568514
- Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, 45, 152–170. doi: 10.1111/j.1469-8986.2007.00602.x
- Frank, M. J., Seeberger, L. C., & O'Reilly, R. C. (2004). By carrot or by stick: Cognitive reinforcement learning in Parkinsonism. *Science*, 306, 1940–1943. doi: 10.1126/science.1102941
- Frank, M. J., Woroch, B. S., & Curran, T. (2005). Error-related negativity predicts reinforcement learning and conflict biases. *Neuron*, 47, 495–501. doi: 10.1016/j.neuron.2005.06.020
- Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9, 474–480. doi: 10.1016/j.tics.2005.08.011
- Friston, K. (2003). Learning and inference in the brain. *Neural Networks*, 16, 1325–1352. doi: 10.1016/j.neunet.2003.06.005
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 360, 815–836. doi: 10.1098/rstb.2005.1622
- Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error-detection and compensation. *Psychological Science*, 4, 385–390.
- Gehring, W. J., & Knight, R. T. (2000). Prefrontal-cingulate interactions in action monitoring. *Nature Neuroscience*, 3, 516–520. doi: 10.1038/74899
- Gevins, A., & Smith, M. E. (2000). Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. *Cerebral Cortex*, 10, 829–839.
- Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, 7, 374–385.
- Gevins, A., Smith, M. E., McEvoy, L. K., Leong, H., & Le, J. (1999). Electroencephalographic imaging of higher brain function. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 354, 1125–1133. doi: 10.1098/rstb.1999.0468
- Gründler, T. O. J., Cavanagh, J. F., Figueroa, C. M., Frank, M. J., & Allen, J. J. B. (2009). Task-related dissociation in ERN amplitude as a function of obsessive-compulsive symptoms. *Neuropsychologia*, 47, 1978–1987. doi: 10.1016/j.neuropsychologia.2009.03.010
- Hajcak, G., Moser, J. S., Yeung, N., & Simons, R. F. (2005). On the ERN and the significance of errors. *Psychophysiology*, 42, 151–160. doi: 10.1111/j.1469-8986.2005.00270.x

- Hanslmayr, S., Pastotter, B., Bauml, K. H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the Stroop task. *Journal of Cognitive Neuroscience*, 20, 215–225. doi: 10.1162/jocn.2008.20020
- Hanslmayr, S., Staudigl, T., Aslan, A., & Bauml, K. H. (2010). Theta oscillations predict the detrimental effects of memory retrieval. *Cognitive, Affective and Behavioral Neuroscience*, 10, 329–338. doi: 10.3758/CABN.10.3.329
- Holroyd, C. B. (2004). A note on the Oddball N200 and the Feedback ERN. In M. F. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts and the brain. Current opinions on performance monitoring* (pp. 211–218). Leipzig, Germany: Max Planck Institute for Human Cognitive and Brain Sciences.
- Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, 109, 679–709.
- Holroyd, C. B., Pakzad-Vaezi, K. L., & Krigolson, O. E. (2008). The feedback correct-related positivity: Sensitivity of the event-related brain potential to unexpected positive feedback. *Psychophysiology*, 45, 688–697. doi: 10.1111/j.1469-8986.2008.00668.x
- Holroyd, C. B., & Yeung, N. (2011). An integrative theory of anterior cingulate cortex function: Option selection in hierarchical reinforcement learning. In R. B. Mars, J. Sallet, M. F. S. Rushworth, & N. Yeung (Eds.), *The neural basis of motivational and cognitive control*. Cambridge, MA: MIT Press.
- Hopfield, J. J. (1982). Neural networks and physical systems with emergent collective computational abilities. *Proceedings of the National Academy of Sciences, USA*, 79, 2554–2558.
- Huster, R. J., Westerhausen, R., Pantev, C., & Konrad, C. (2010). The role of the cingulate cortex as neural generator of the N200 and P300 in a tactile response inhibition task. *Human Brain Mapping*, 31, 1260–1271. doi: 10.1002/hbm.20933
- Ishii, R., Shinosaki, K., Ukai, S., Inouye, T., Ishihara, T., Yoshimine, T., . . . Takada, M. (1999). Medial prefrontal cortex generates frontal midline theta rhythm. *NeuroReport*, 10, 675–679.
- Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: Theta correlates of memory retrieval and decision making. *NeuroImage*, 32, 978–987. doi: 10.1016/j.neuroimage.2006.02.018
- Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience*, 15, 1395–1399.
- Kahana, M. J., Sekuler, R., Caplan, J. B., Kirschen, M., & Madsen, J. R. (1999). Human theta oscillations exhibit task dependence during virtual maze navigation. *Nature*, 399, 781–784. doi: 10.1038/21645
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research, Brain Research Reviews*, 29, 169–195.
- Klimesch, W., Doppelmayr, M., Schwaiger, J., Winkler, T., & Gruber, W. (2000). Theta oscillations and the ERP old/new effect: Independent phenomena? *Clinical Neurophysiology*, 111, 781–793.
- Klimesch, W., Sauseng, P., Hanslmayr, S., Gruber, W., & Freunberger, R. (2007). Event-related phase reorganization may explain evoked neural dynamics. *Neuroscience and Biobehavioral Reviews*, 31, 1003–1016. doi: 10.1016/j.neubiorev.2007.03.005
- Lachaux, J. P., Rodriguez, E., Martinerie, J., & Varela, F. J. (1999). Measuring phase synchrony in brain signals. *Human Brain Mapping*, 8, 194–208. doi: 10.1002/(SICI)1097-0193(1999)8:4<194::AID-HBM4>3.0.CO;2-C
- Le Van Quyen, M., & Bragin, A. (2007). Analysis of dynamic brain oscillations: Methodological advances. *Trends in Neuroscience*, 30, 365–373. doi: 10.1016/j.tins.2007.05.006
- Leung, L. W., & Borst, J. G. (1987). Electrical activity of the cingulate cortex. I. Generating mechanisms and relations to behavior. *Brain Research*, 407, 68–80. doi: 10.1016/0006-8993(87)91220-0
- Luu, P., & Tucker, D. M. (2001). Regulating action: Alternating activation of midline frontal and motor cortical networks. *Clinical Neurophysiology*, 112, 1295–1306.
- Luu, P., Tucker, D. M., Derryberry, D., Reed, M., & Poulsen, C. (2003). Electrophysiological responses to errors and feedback in the process of action regulation. *Psychological Science*, 14, 47–53.
- Luu, P., Tucker, D. M., & Makeig, S. (2004). Frontal midline theta and the error-related negativity: Neurophysiological mechanisms of action regulation. *Clinical Neurophysiology*, 115, 1821–1835. doi: 10.1016/j.clinph.2004.03.031
- Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends in Cognitive Sciences*, 8, 204–210. doi: 10.1016/j.tics.2004.03.008
- Marco-Pallares, J., Cucurell, D., Cunillera, T., Garcia, R., Andres-Pueyo, A., Munte, T. F., & Rodríguez-Fornells, A. (2008). Human oscillatory activity associated to reward processing in a gambling task. *Neuropsychologia*, 46, 241–248. doi: 10.1016/j.neuropsychologia.2007.07.016
- Mulert, C., Menzinger, E., Leicht, G., Pogarell, O., & Hegerl, U. (2005). Evidence for a close relationship between conscious effort and anterior cingulate cortex activity. *International Journal of Psychophysiology*, 56, 65–80. doi: 10.1016/j.ijpsycho.2004.10.002
- Mulert, C., Seifert, C., Leicht, G., Kirsch, V., Ertl, M., Karch, S., . . . Jäger, L. (2008). Single-trial coupling of EEG and fMRI reveals the involvement of early anterior cingulate cortex activation in effortful decision making. *NeuroImage*, 42, 158–168. doi: 10.1016/j.neuroimage.2008.04.236
- Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, 15, 1–25. doi: 10.1002/hbm.1058
- Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and Biobehavioral Reviews*, 34, 1023–1035. doi: 10.1016/j.neubiorev.2009.12.014
- Olvet, D. M., & Hajcak, G. (2008). The error-related negativity (ERN) and psychopathology: Toward an endophenotype. *Clinical Psychology Review*, 28, 1343–1354. doi: 10.1016/j.cpr.2008.07.003
- Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *NeuroImage*, 27, 341–356. doi: 10.1016/j.neuroimage.2005.04.014
- O'Reilly, R. C., & Munakata, Y. (2000). *Computational explorations in cognitive neuroscience: Understanding the mind by simulating the brain*. Cambridge, MA: MIT Press.
- Overbeek, T. J. M., Nieuwenhuis, S., & Ridderinkhof, K. R. (2005). Dissociable components of error processing: On the functional significance of the Pe vis-a-vis the ERN/Ne. *Journal of Psychophysiology*, 19, 319–329. doi: 10.1027/0269-8803.19.4.319
- Pailing, P. E., & Segalowitz, S. J. (2004). The effects of uncertainty in error monitoring on associated ERPs. *Brain and Cognition*, 56, 215–233. doi: 10.1016/j.bandc.2004.06.005
- Paus, T. (2001). Primate anterior cingulate cortex: Where motor control, drive and cognition interface. *Nature Reviews Neuroscience*, 2, 417–424. doi: 10.1038/35077500
- Raghavachari, S., Lisman, J. E., Tully, M., Madsen, J. R., Bromfield, E. B., & Kahana, M. J. (2006). Theta oscillations in human cortex during a working-memory task: Evidence for local generators. *Journal of Neurophysiology*, 95, 1630–1638. doi: 10.1152/jn.00409.2005
- Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science*, 306, 443–447. doi: 10.1126/science.1100301
- Ritter, P., & Becker, R. (2009). Detecting alpha rhythm phase reset by phase sorting: Caveats to consider. *NeuroImage*, 47, 1–4. doi: 10.1016/j.neuroimage.2009.04.031
- Rizzuto, D. S., Madsen, J. R., Bromfield, E. B., Schulze-Bonhage, A., & Kahana, M. J. (2006). Human neocortical oscillations exhibit theta phase differences between encoding and retrieval. *NeuroImage*, 31, 1352–1358. doi: 10.1016/j.neuroimage.2006.01.009
- Rizzuto, D. S., Madsen, J. R., Bromfield, E. B., Schulze-Bonhage, A., Seelig, D., Aschenbrenner-Scheibe, R., & Kahana, M. J. (2003). Reset of human neocortical oscillations during a working memory task. *Proceedings of the National Academy of Sciences, USA*, 100, 7931–7936. doi: 10.1073/pnas.0732061100
- Rushworth, M. F., Buckley, M. J., Behrens, T. E., Walton, M. E., & Bannerman, D. M. (2007). Functional organization of the medial frontal cortex. *Current Opinion in Neurobiology*, 17, 220–227. doi: 10.1016/j.conb.2007.03.001
- Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience and Biobehavioral Reviews*, 34, 1015–1022. doi: 10.1016/j.neubiorev.2009.12.006
- Sauseng, P., Klimesch, W., Doppelmayr, M., Hanslmayr, S., Schabus, M., & Gruber, W. R. (2004). Theta coupling in the human electroencephalogram during a working memory task. *Neuroscience Letters*, 354, 123–126.
- Sauseng, P., Klimesch, W., Gruber, W. R., Hanslmayr, S., Freunberger, R., & Doppelmayr, M. (2007). Are event-related potential components generated by phase resetting of brain oscillations? A critical discussion.

- Neuroscience, 146, 1435–1444. doi: 10.1016/j.neuroscience.2007.03.014
- Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience*, 12, 154–167. doi: 10.1038/nrn2994
- Simon, J. R., & Rudell, A. P. (1967). Auditory S-R compatibility: The effect of an irrelevant cue on information processing. *Journal of Applied Psychology*, 51, 300–304.
- Staudigl, T., Hanslmayr, S., & Bauml, K. H. (2010). Theta oscillations reflect the dynamics of interference in episodic memory retrieval. *Journal of Neuroscience*, 30, 11356–11362. doi: 10.1523/JNEUROSCI.0637-10.2010
- Sutton, R. S., & Barto, A. G. (1998). *Reinforcement learning: An introduction*. Cambridge, MA: MIT Press.
- Swick, D., & Turken, U. (2002). Dissociation between conflict detection and error monitoring in the human anterior cingulate cortex. *Proceedings of the National Academy of Sciences, USA*, 99, 16354–16359. doi: 10.1073/pnas.252521499
- Talairach, J., Bancaud, J., Geier, S., Bordas-Ferrer, M., Bonis, A., Szikla, G., & Rusu, M. (1973). The cingulate gyrus and human behaviour. *Electroencephalography and Clinical Neurophysiology*, 34, 45–52.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1997). Oscillatory gamma-band (30–70 Hz) activity induced by a visual search task in humans. *Journal of Neuroscience*, 17, 722–734.
- Trujillo, L. T., & Allen, J. J. (2007). Theta EEG dynamics of the error-related negativity. *Clinical Neurophysiology*, 118, 645–668. doi: 10.1016/j.clinph.2006.11.009
- Tsujimoto, T., Shimazu, H., & Isomura, Y. (2006). Direct recording of theta oscillations in primate prefrontal and anterior cingulate cortices. *Journal of Neurophysiology*, 95, 2987–3000. doi: 10.1152/jn.00730.2005
- Ullsperger, M., & von Cramon, D. Y. (2006). The role of intact frontostriatal circuits in error processing. *Journal of Cognitive Neuroscience*, 18, 651–664. doi: 10.1162/jocn.2006.18.4.651
- Van Veen, V., & Carter, C. S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience*, 14, 593–602. doi: 10.1162/08989290260045837
- Vidal, F., Burle, B., Bonnet, M., Grapperon, J., & Hasbroucq, T. (2003). Error negativity on correct trials: A reexamination of available data. *Biological Psychology*, 64, 265–282.
- Vidal, F., Hasbroucq, T., Grapperon, J., & Bonnet, M. (2000). Is the ‘error negativity’ specific to errors? *Biological Psychology*, 51, 109–128.
- Vogt, B. A. (2005). Pain and emotion interactions in subregions of the cingulate gyrus. *Nature Reviews Neuroscience*, 6, 533–544. doi: 10.1038/nrn1704
- Wang, C., Ulbert, I., Schomer, D. L., Marinkovic, K., & Halgren, E. (2005). Responses of human anterior cingulate cortex microdomains to error detection, conflict monitoring, stimulus-response mapping, familiarity, and orienting. *Journal of Neuroscience*, 25, 604–613. doi: 10.1523/JNEUROSCI.4151-04.2005
- Womelsdorf, T., Johnston, K., Vinck, M., & Everling, S. (2010). Theta-activity in anterior cingulate cortex predicts task rules and their adjustments following errors. *Proceedings of the National Academy of Sciences, USA*, 107, 5248–5253. doi: 10.1073/pnas.0906194107
- Womelsdorf, T., Schoffelen, J. M., Oostenveld, R., Singer, W., Desimone, R., Engel, A. K., & Fries, P. (2007). Modulation of neuronal interactions through neuronal synchronization. *Science*, 316, 1609–1612. doi: 10.1126/science.1139597
- Womelsdorf, T., Vinck, M., Leung, L. S., & Everling, S. (2010). Selective theta-synchronization of choice-relevant information subserves goal-directed behavior. *Frontiers in Human Neuroscience*, 4, 210. doi: 10.3389/fnhum.2010.00210
- Yeung, N., Bogacz, R., Holroyd, C. B., & Cohen, J. D. (2004). Detection of synchronized oscillations in the electroencephalogram: An evaluation of methods. *Psychophysiology*, 41, 822–832. doi: 10.1111/j.0048-5772.2004.00239.x
- Yeung, N., Bogacz, R., Holroyd, C. B., Nieuwenhuis, S., & Cohen, J. D. (2007). Theta phase resetting and the error-related negativity. *Psychophysiology*, 44, 39–49. doi: 10.1111/j.1469-8986.2006.00482.x
- Yeung, N., Botvinick, M. M., & Cohen, J. D. (2004). The neural basis of error detection: Conflict monitoring and the error-related negativity. *Psychological Review*, 111, 931–959. doi: 10.1037/0033-295X.111.4.939
- Yordanova, J., Falkenstein, M., Hohnsbein, J., & Koev, V. (2004). Parallel systems of error processing in the brain. *NeuroImage*, 22, 590–602. doi: 10.1016/j.neuroimage.2004.01.040
- Zirnheld, P. J., Carroll, C. A., Kieffaber, P. D., O’Donnell, B. F., Shekhar, A., & Hetrick, W. P. (2004). Haloperidol impairs learning and error-related negativity in humans. *Journal of Cognitive Neuroscience*, 16, 1098–1112. doi: 10.1162/0898929041502779

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1: Paired *t* test data from Figure 8

Table S2: Factor analysis results of raw EEG data

Figure S1: Broadband (0.05–15 Hz) ERPs at the FCz electrode, overlapped within each condition.

Figure S2: Delta band (1–4 Hz) ERPs at the FCz electrode.

Figure S3: Alpha band (1–4 Hz) ERPs at the FCz electrode.

Figure S4: Beta band (1–4 Hz) ERPs at the FCz electrode.

Figure S5: Stimulus-locked topoplots as shown in Figure 3 of the main text (average reference), with additional artifact rejection ($\pm 100 \mu\text{V}$ at FP1) or with an alternative reference scheme (linked mastoids). These plots demonstrate that frontal and occipital theta power seen in the topoplots are a feature of the averaged reference and are not due to artifact contamination.

Figure S6: Response-locked topoplots as shown in Figure 4 with variants as above.

Figure S7: Stimulus-locked topoplots as shown in Figure 6 with variants as above.

Figure S8: Response-locked topoplots as shown in Figure 7 with variants as above.

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